Norwegian University of Life Sciences
Faculty of Environmental Science and Technology
Department of Ecology
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2016:36

Game Vertebrate Responses to Rural Populations in Neotropical Protected Areas

Viltets respons på lokalbefolkningens aktivitet i neotropiske verneområder

Whaldener Endo

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"The day has passed delightfully. Delight itself, however, is a weak term to express the feelings of a naturalist who, for the first time, has wandered by himself in a Brazilian forest. [...] To a person fond of natural history, such a day as this brings with it a deeper pleasure than he can ever hope to experience again." Charles Darwin, The Voyage of the Beagle

Ås, February 2016
Whaldener Endo

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Papers I to IV

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Endo, W., Peres, C. A., Haugaasen, T. Seasonal variation in animal protein acquisition by semi-subsistence Amazonians in floodplain settlements.
Biological Conservation, in revision

Paper II
Endo, W., Peres, C. A., Salas, E., Mori, S., Sanchez-Vega, J. l., Shepard, G. H., Yu, D. W. (2010). Game vertebrate densities in hunted and nonhunted forest sites in Manu National Park, Peru. *Biotropica* 42(2), 251-261
DOI:10.1111/j.1744-7429.2009.00546.x

Paper III
Endo, W., Morato, R. G., da Cunha, F. P., Beisiegel, B. M., Peres, C. A.
Anthropogenic and environmental correlates of medium- to large-bodied mammal occupancy in protected areas of the Brazilian Caatinga. *To be submitted to Biodiversity and Conservation*

Paper IV
Endo, W., Peres, C. A., Haugaasen, T. (2014). Seasonal abundance and breeding habitat occupancy of the Orinoco Goose (*Neochen jubata*) in western Brazilian Amazonia. *Bird Conservation International* 24(4): 518-529.
DOI:10.1017/S0959270914000173

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Wiley: Paper II
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Abstract

Medium- to large-bodied vertebrates are of critical importance to the integrity of natural ecosystems, sustaining the composition and structure of plant and faunal communities and the associated ecosystem services. Through distinct mechanisms, such as competition, predation and trophic cascades, they are able to promote profound influences across the entire plant and faunal community structure. These vertebrate species are often game vertebrates of great importance for local subsistence and cash, as they may serve as essential sources of food and other byproducts, particularly for human populations in rural areas. Despite their importance, game vertebrates have been severely impacted by human activities, and even natural areas with small, sparse rural populations are also likely to have their game populations affected by anthropogenic factors.

This thesis aims to investigate the patterns of subsistence hunting practiced by human populations living within or in the vicinity of natural protected areas and how hunting and related anthropogenic activities affect local game communities. The study also attempts to shed light on the effectiveness of protected areas in maintaining viable populations of medium- to large-bodied vertebrates. To advance these goals, game vertebrate populations occurring at eight distinct South American protected areas were surveyed using line-transect censuses, camera-trapping surveys and censuses along rivers. Moreover, influences of local human populations on game communities were assessed by conducting household interviews and gathering information on other activities practiced by these rural populations.

The occurrence of a large assemblage of game species in all surveyed sites is a resounding confirmation of the importance of protected areas for biodiversity conservation. Yet, the results also provided evidence that game vertebrate communities within these protected areas are being significantly affected by local human populations, with areas under different levels of influence of human activities diverging in the structure and composition of game communities.

The claim that hunting is likely to be a major factor altering game populations in natural areas was corroborated by this study. However, the results also showed that game populations are greatly affected by other activities associated with rural populations. Overgrazing from cattle husbandry activities were related to lower occupancies of the most vulnerable game species surveyed, whereas compensatory modes of animal protein acquisition such as fishing was found to have a strong influence on hunting patterns, thereby indirectly affecting game offtake levels in some surveyed sites. These results underline the inter-relationship and synergistic effects of such activities, and the need to account for all the different aspects of rural livelihoods in ensuring the long-term persistence of neotropical game vertebrates.

Sammendrag

Mellomstore og store virveldyr har en avgjørende betydning for særpreget til naturlige økosystemer. De er med på å opprettholde sammensetning og struktur av de ulike plante- og dyresamfunnene, og tilhørende økosystemtjenester. Gjennom ulike mekanismer, som for eksempel konkurranse og predasjon, har de stor innflytelse over strukturen til hele plante- og dyresamfunn. Mange virveldyrarter er ofte av stor betydning for menneskers tilværelse og økonomi. De kan være viktige som matkilder og andre biprodukter, særlig blant befolkninger i rurale strøk. Til tross for sin store betydning, har mange små- og storviltpopulasjoner blitt sterkt negativt påvirket av menneskelig aktivitet. Til og med i naturområder med små, spredte, rurale befolkninger er det sannsynlig at mange viltbestander påvirkes av menneskelig aktivitet.

Denne oppgaven tar sikte på å undersøke jaktmønstrene til mennesker som lever innenfor eller i nærheten av naturvernområder, og hvordan jakt og annen menneskelig aktivitet påvirker lokale viltpopulasjoner. Studien forsøker også å belyse betydningen av naturvernområder for å opprettholde levedyktige bestander av viltpopulasjoner. For å undersøke dette ble det brukt transekttellinger, viltkameraundersøkelser og tellinger langs elver for å kartlegge viltbestander i åtte forskjellige søramerikanske naturreservater. Videre ble lokalbefolkningens påvirkning av viltpopulasjoner undersøkt ved intervjuer i husstander og ved å samle informasjon om andre aktiviteter utført av den rurale befolkningen.

Høy konsentrasjon av mange viltarter i de undersøkte områdene er en god bekreftelse på at naturvernområder er viktig for bevaring av biologisk mangfold. Resultatene viser likevel også at viltsamfunn i mange av disse verneområdene blir vesentlig påvirket av lokalbefolkningen. Viltsamfunn i områder med ulik grad av menneskelig påvirkning viser seg å ha forskjellig struktur og sammensetning.

Påstanden om at jakt kan være en viktig faktor for å redusere viltbestander i naturområder ble bekreftet i dette studiet. Resultatene viste imidlertid at viltbestander også kan være sterkt påvirket av andre aktiviteter knyttet til den rurale befolkningen. Overbeiting av storfe hadde stor negativ betydning for de mest sårbare viltartene som ble undersøkt. Utnyttelse av alternative animalske proteinkilder, for eksempel fra fisk, hadde sterk innflytelse på jaktmønstre, og påvirket dermed indirekte mengden vilt som ble jaktet i enkelte av områdene. Disse resultatene

understreker forholdet og synergieffektene mellom ulike aktiviteter og behovet for å ta hensyn til de forskjellige aspektene av levekår i rurale strøk for å sikre den langsiktige bevaringen av neotropiske viltbestander.

Resumo

Vertebrados de médio e grande porte são fundamentais para a integridade de ecossistemas naturais, sustentando a composição e estrutura de comunidades de plantas e animais, bem como os serviços ecossistêmicos associados. Através de mecanismos distintos, como competição, predação e cascatas tróficas, eles podem promover profundas influências ao longo de toda a estrutura da comunidade de plantas e animais. Essas espécies de vertebrados são frequentemente cinegéticas de grande importância para a subsistência e renda local, por servirem como fontes essenciais de alimento e outros subprodutos, sobretudo em áreas rurais. Apesar de sua importância, vertebrados cinegéticos vêm sendo severamente impactados por atividades humanas, e mesmo em áreas com pequenas e esparsas populações rurais é possível que populações locais da fauna cinegética sejam afetadas por fatores antropogênicos.

Esta tese busca investigar os padrões da caça de subsistência praticada por populações humanas que vivem dentro ou nos arredores de área protegidas naturais, e entender como a caça e outras atividades antropogênicas relacionadas afetam a fauna cinegética local. O estudo também busca gerar uma maior clareza na eficácia das áreas protegidas para a manutenção de populações viáveis de vertebrados de médio e grande porte. Para avançar nestas propostas, as populações de vertebrados cinegéticos de oito áreas protegidas distintas da América do Sul foram amostradas, por meio censos em transectos lineares, amostragens com armadilhamento fotográfico e censos ao longo de rios. Além disso, as influências de populações humanas locais sobre comunidades da fauna cinegética também foram investigadas através de entrevistas domiciliares e do recolhimento de informações sobre outras atividades praticadas por essas populações rurais.

A ocorrência de uma grande assembléia de espécies cinegéticas em todas as áreas amostradas é uma contundente confirmação da importância de áreas protegidas para a conservação da biodiversidade. No entanto, os resultados também demostraram que comunidades de vertebrados cinegéticos presentes dentro destas áreas protegidas vêm sendo significativamente afetadas pelas populações humanas locais, pois áreas sob diferentes niveis de influência de atividades humanas divergiram na estrutura e composição das comunidades de fauna cinegética existentes.

O argumento de que a caça é possivelmente um dos principais fatores de alteração de populações de espécies cinegéticas em áreas naturais foi corroborado por este estudo. No entanto, os resultados também demonstraram que populações cinegéticas são fortemente afetadas por outras atividades associadas com as populações rurais. O sobrepastoreio de atividades pecuárias foram relacionadas a baixas ocupâncias das espécies cinegéticas mais vulneráveis, enquanto métodos compensatórios de aquisição de proteina animal, como a pesca, demonstraram exercer uma forte influência nos padrões de caça, afetando indiretamente os níveis de obtenção de caça em algumas das áreas amostradas. Esses resultados evidenciam a inter-relação e os efeitos sinergísticos destas atividades, e a necessidade de se levar em conta todos os diferentes aspectos dos modos de vida das populações rurais, de modo a garantir a persistência ao longo-prazo dos vertebrados cinegéticos neotropicais.

SYNOPSIS


Photo: W. Endo

1. Introduction

1.1 Game vertebrates and their importance in natural ecosystems

Game vertebrates, here defined as medium- and large-sized reptiles, birds and mammals commonly hunted by human populations, are of critical importance to the maintenance of natural ecosystems. Through a vast plethora of distinct functional roles, they directly and indirectly (e.g. via trophic cascades) sustain the composition and structure of plant and faunal communities and, thereby, the myriad of ecosystem services associated to these species (Estes et al. 2011, Terborgh and Estes 2010).

Changes in game community structure are likely to eventually cause profound transformations across the entire trophic structure of the ecosystems where they occur (Wright 2003, Muller-Landau 2007, Estes et al. 2011). More specifically, declines in game populations are generally known to affect other vertebrates through processes related to competition and predation (e.g. Ripple and Beschta 2011). One celebrated example on how predation, herbivory and competition by large vertebrates may affect other vertebrate populations can be seen in Yellowstone National Park, USA. Elk populations living within the park boundaries suffered a steep decline in their abundance and marked changes in their foraging activities due to a reintroduction of wolves, whereas beaver, bison and a myriad of smaller vertebrate species experienced an increase in their populations because of a decrease in elk overgrazing, particularly along riparian areas (Ripple and Beschta 2012).

Herbivore game vertebrates are important agents controlling plant populations and shaping plant community structure. By feeding on fruits, frugivores may act as efficient seed dispersers, promoting the development and establishment of a vast array of plant species (Stoner et al. 2007, Wang et al. 2007, Brodie et al. 2009, Holbrook and Loiselle 2009). The lowland tapir (*Tapirus terrestris*) is an example of a highly pursued game species known to be a high-quality seed disperser of more than 30 different plant species (Salas and Fuller 1996, Fragoso and Huffman 2000, Henry et al. 2000). In tropical forests, primates are also important frugivores dispersing large quantities of seeds of fruit-bearing plant species, particularly those with large diaspores (Chapman 1989, Eisenberg and Thorington 1973). Granivorous game vertebrates, on the other hand, are known to control plant populations by intensifying the rate of seed predation (Roldán and Simonetti 2001, Stoner et al. 2007, Wang et al. 2007). Yet, by scatter-hoarding large numbers of seeds they may also act as seed dispersers and move seeds at considerable distances away from the parent plant, greatly improving the chances of a given seed to successfully develop into seedlings or larger individuals (Janzen 1970). Agoutis (*Dasyprocta* spp.), for example, are able to disperse Brazil nut seeds up to 60m away from their parent trees (Tuck Haugaasen et al. 2011). In the later stages of plant development, large browsers and grazers may also control plant populations by reducing the recruitment of tree species or the survival rate of damaged individuals (MacDougall 2008, Nunez-Iturri et al. 2008, Vanthomme et al. 2010, Effiom et al. 2013).

Due to various top-down forms of floristic control by herbivores, sites with a history of intense hunting pressure are likely to present a lower species richness and density of game-dispersed plant species compared to unhunted sites, and an increase in the richness and abundance of plant species dispersed by non-game species or abiotic means (Nuñez-Iturri 2007). Declines in the large vertebrate community is also likely to negatively affect the genetic pool of plant species dispersed by game vertebrates, by reducing the gene flow and leading to lower genetic differentiation (Pacheco and Simonetti 2000).

Game populations are also providers of vital resources to distinct taxonomic groups, underlining their importance in maintaining the integrity of natural ecosystems. Dung beetle assemblages, for example, are known to contain a different set of species in overhunted areas due to changes in the availability of fecal resources from large game species (Vulinec et al. 2006, Nichols et al. 2013). These resources may not be exclusively related to trophic interactions. White-lipped peccaries in neotropical forests, for example, are known to supply anurans with important reproduction sites by creating earth wallows while foraging (Beck et al. 2010).

Since game vertebrates are so important in maintaining the integrity of natural ecosystems, severe impacts on this group are likely to produce profound large-scale implications to natural ecosystems. The fact that game vertebrates are also important to global scale ecosystem services, such as carbon storage (Boettcher and Hoffmann 2009, Bello et al. 2015, Peres et al. 2016) and nutrient concentration gradients (Wolf et al. 2013), underlines the need of further assessing the current status of game populations worldwide, and how they are impacted by human populations.

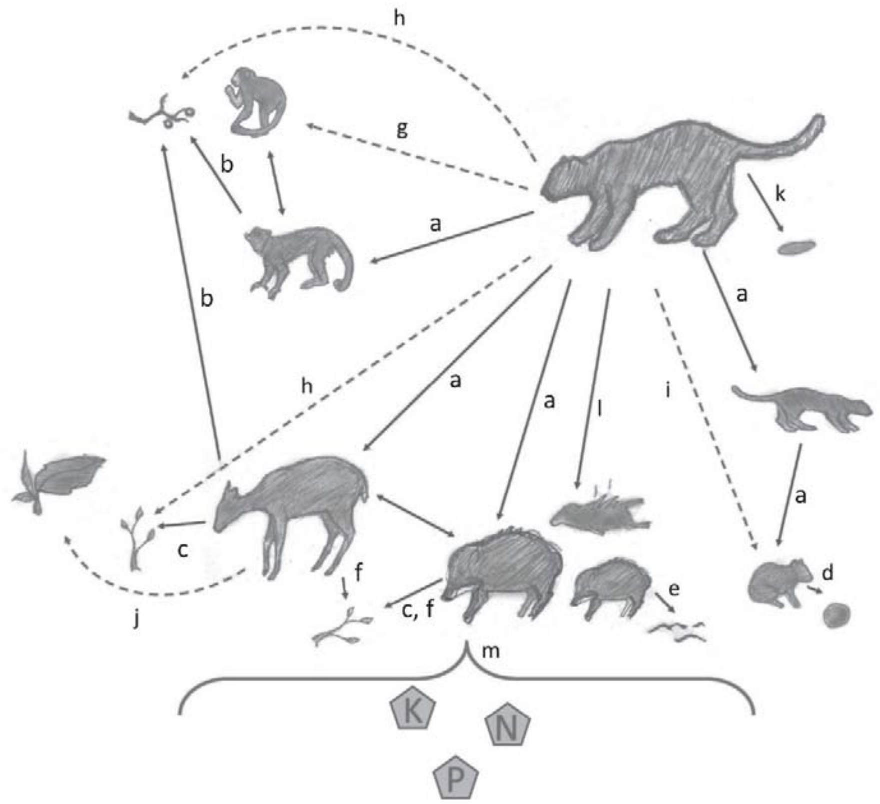

Figure 1. Examples of ecosystem services provided by game vertebrates: a. predation affecting prey survival (e.g. Post et al. 1999, Terborgh et al. 2001, Estes et al. 2011, Newsome and Ripple 2015) ; b. frugivory affecting plant recruitment (e.g. Ickes et al. 2001); c. browsing and grazing affecting plant survival (e.g. Terborgh et al. 2001); d. Granivory affecting plant recruitment; (e.g. Asquith et al. 1997, 1999, Silman et al. 2003) e. Ecosystem engineering (e.g. Pringle 2008, Beck et al. 2010, Pike and Mitchell 2013); f. Trampling and other physical actions affecting plant recruitment and survival (e.g. Ickes et al. 2001); g. predation affecting prey competitor population (e.g. Newsome and Ripple 2015); h. Predation of herbivores indirectly affecting plant population (e.g. Post et al. 1999, Terborgh et al. 2001); i. Mesopredator release affecting lesser prey populations (e.g. Letnic et al. 2009, Newsome and Ripple 2015); j. Herbivory indirectly affecting populations of other competing plant species; k. Fecal production affecting detritivorous populations (Nichols et al. 2009, Nichols et al. 2013); l. Predation affecting scavenger populations (e.g. Wilson and Wolkovich 2011, Field and Reynolds 2013); m. Large vertebrates affecting ecosystem nutrient concentration gradient (e.g. Doughty et al. 2013a, b, Wolf et al. 2013). *Artwork: W. Endo*

1.2 Game vertebrates and human populations in tropical ecosystems

Hunting is one of the oldest forms of protein acquisition by human populations (Thieme 1997), and is still widely practiced worldwide, especially in areas with poor access to industrialized products. In the tropics, where rural populations are often heavily dependent on natural resources, hunting is an important activity (e.g. Noss 1997, Noss 1998, Carpaneto and Fusari 2000, Souza-Mazurek 2000, Cullen Jr. et al. 2001, Fa et al. 2002, Fa and Peres 2002, Riley 2002, Kaul et al. 2004, Kumara and Singh 2004, Fa et al. 2005, Rao et al. 2005, Fa et al. 2006, León and Montiel 2008, Golden 2009, Zapata-Ríos et al. 2009, Randrianandrianina et al. 2010, Martin et al. 2012, Pangau-Adam et al. 2012, Velho et al. 2012). In tropical areas, hunting is essentially practiced as a form of food acquisition by rural populations, supplying the extractors with invaluable intake of protein and fat. Additionally, hunters also pursue game species for other purposes (Mittermeier 1987), including the use of animal parts for clothing and ornaments (Van Den Bergh et al. 2013), leisure (Trinca et al. 2007), retaliation, taming or domestication of young individuals (Van Den Bergh et al. 2013), and pest control (Wadley et al. 1997, Smith 2005). This extractive activity is part of an important set of social and cultural values and codes, often strengthening social bonds and their integrity (e.g. Hawkes et al. 2001, Young et al. 2001, Tadie and Fischer 2013). Hunting can also be an important source of income for many rural populations worldwide (Fitzgibbon et al. 1995, Juste et al. 1995, Wilkie and Carpenter 1999, Edderai and Dame 2006, Kümpel et al. 2010, Wright and Priston 2010, Nasi et al. 2011), in many areas frequently surpassing household consumption in its importance (de Merode et al. 2004).

Given that rural human populations often depend so heavily on the outcomes of hunting, the conservation of game populations is a subject of high social concern. Negative impacts on game species, which include game population declines and extinctions, are likely to compromise the food security of many human populations that rely on this resource to supply their nutritional needs, and to dismantle the integrity of their cultural system.

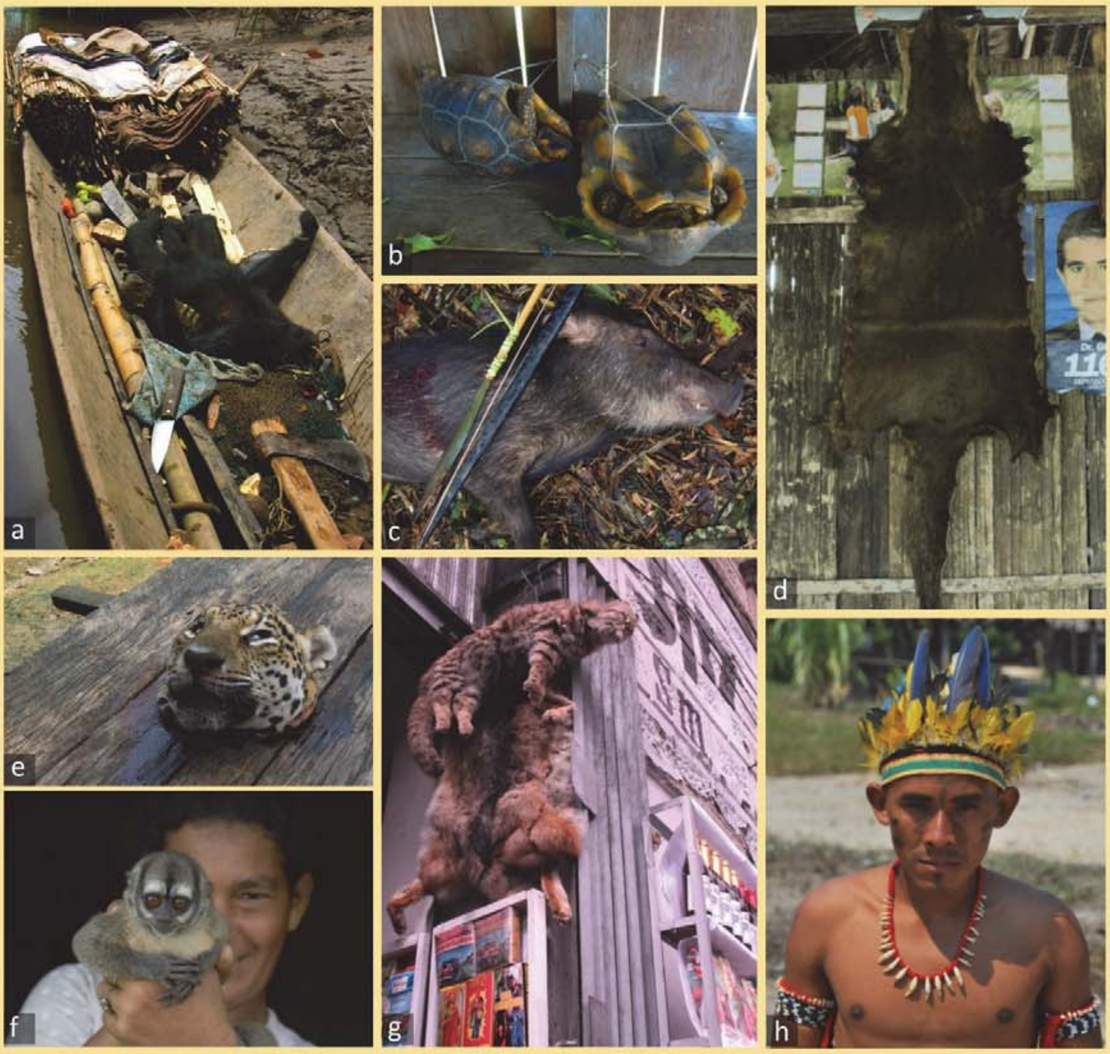

Figure 2. Examples of hunting purposes in the tropics:

Food Acquisition: (a, c) spider-monkey (*Ateles chamek*) and white-lipped peccary (*Tayassu pecari*) caught by Matsigenka hunters at Manu National Park, Perú; (b) tortoises (*Geochelone denticulata*) captured for food consumption at Uacari Sustainable Development Reserve, Brazil;

Trophy: (d) Giant otter (*Pteronura brasiliensis*) pelt at a house in the Uacari Sust. Dev. Res., Brazil;

Retaliation: (e) jaguar (*Panthera onca*) killed by village hunters for attacking domestic pigs at the Uacari Sust. Dev. Res., Brasil.

Pet-keeping: (f) Nigh-monkey (*Aotus nancymae*) kept as a pet at the Uacari Sust. Dev. Res., Brazil.

Religious and Medicinal purposes: (g) killed carnivores (*Leopardus jacobita* and *Lycalopex culpeo*) being sold at La Paz, Bolivia.

Ornament: (h) young Deni man wearing diadema, necklace and bracelets made of macaw feathers and primate teeth at the Deni Indigenous Territory, Brazil. *Photos: W. Endo*

1.3. Hunting patterns

Hunters may change their foraging patterns according to internal and external factors. For example, when other sources of protein, such as fish, domestic livestock or preprocessed food are available, hunters may select these items instead of bushmeat (Jenkins et al. 2011, Nielsen 2006). These alternative sources of food may, in this way, positively influence the sustainability of hunting by constraining hunting activities. Conversely, declines or removal of alternative sources are likely to increase the dependence of hunters on bushmeat, thereby intensifying hunting activities.

Hunters also use a great number of different landscapes in order to maximize the energy return from hunting (Parry et al 2009). Hunters may even use secondary forests since some species benefit from such kinds of altered landscapes (Linares 1976). Spatial and temporal changes in the availability of prey for hunters may also affect a hunter's foraging patterns. The seasonal inundation of large areas of floodplain forests in the Amazon, for example, affects the permanence of land vertebrates in these areas. The seasonal migration of several migratory fluvial beach birds restricts the breeding seasons of these species to a few months of the year (see Paper I and IV; Davenport et al. 2012).

Notwithstanding the selective behaviour of hunters, species with life history characteristics that make them more susceptible to hunter detection or encounters with humans may increase the occurrence of opportunistic hunting. Species that are attracted to resources found in areas with intense human use, for example, are likely to be targeted.

Although several hunting societies have long extracted prey populations without compromising their long-term persistence, current environmental, social and socioeconomic changes are progressively undermining the viability of such practices (Kumara and Singh 2004). The shift from traditional hunting technologies to more modern and efficient weapons is a well-known example of a process promoting profound impacts on the sustainability of hunting in several areas (Hames 1979, Damania et al. 2005). In less than three decades, the Huaoroni people of Ecuador switched their hunting patterns from an extractive activity relying on traditional hunting technologies, such as blowguns and spears, to a hunting society where virtually all hunters now use shotguns (Yost and Kelley 1983, Franzen 2006). Other common cultural changes often resulting in negative influences include more sedentary settlements in response to health outposts and schools (Jerozolimski and Peres

2003), engagement of rural populations with bushmeat trade (Bowen-Jones and Pendry 1999, Cowlishaw et al. 2005), and increasing use of motorized boats and vehicles (Souza-Mazurek et al. 2000). Even at the household level, different characteristics may influence the level of hunting, including household size, distance of settlements to protected areas, household wealth, and level of education (Foerster et al. 2011).

1.4. Influences of hunting on game vertebrate populations in tropical ecosystems

Game vertebrates are frequently harvested at unsustainable levels (e.g. Wilkie et al. 1998a, Fa et al. 2003, Refisch 2005, Thiollay 2005, Bennet et al. 2006, Struebig et al. 2007, Kümpel et al. 2008, Phoonjampa and Brockelman 2008, Pailler et al. 2009, de Thoisy et al. 2009, Rist et al. 2009, Topp-Jørgensen et al. 2009). The trade and consumption of bushmeat is one of the main drivers of population declines and local extinctions throughout the tropics (e.g. Pilgram and Western 1986, Wich et al. 2011), and may frequently cause stronger impacts on game populations than habitat loss or degradation *per se* (Wilkie et al. 1998a, 1998b, Rovero et al. 2012). Even when hunted populations can persist, the reduction in genetic diversity may weaken the long-term viability of these exploited populations (Ryman et al. 1981).

Hunters may act as selective predators, pursuing preferred prey more intensively, thereby increasing the vulnerability of exploited populations (Milner et al. 2007, Nasi et al. 2011). In general, large-bodied species provide better foraging returns to hunters and are therefore more frequently pursued. Yet, larger species are usually those with lower intrinsic rates of population increase (Fenchel 1974) and are more likely to be severely impacted by such threats. Ungulates, for example, are usually the most preferred game species in the tropics, and while a few ungulate species seem to be resilient to moderate levels of hunting pressure (e.g. brocket deer) most ungulates in the tropics are vulnerable to hunting (Hurtado-Gonzales and Bodmer 2004, Peres and Palacios 2007). Curassows, as many members of the Galliformes, are heavily pursued large birds in the Neotropical region and are likely impacted by hunting pressure (Keane et al. 2005). This variation in prey offtake levels is likely to promote changes in the game community composition. Moreover, because hunters also select certain types of individuals from a single population they can also affect the age structure and sex ratio of exploited populations (Sabrina et al. 2009, Darimont and Child 2014).

Hunting is frequently seen as an altogether detrimental activity to land vertebrates. However, because hunters are selective foragers, and because each game species possess distinct traits, the resilience of exploited populations to the impacts of hunting varies considerably (Peres and Palacios 2007, Linder and Oates 2010). The fast reproductive rate of agoutis and other large rodents, for example, render them less vulnerable than species with a lower reproductive rate, such as tapirs and large primates, to more intensive hunting activities (Robinson and Redford 1986). Competing species may even be favoured by declines in the abundance of its competitors due to hunting, thereby becoming more abundant in selectively overhunted areas (Peres and Dolman 2000).

Conceptually, game populations are harvested unsustainably when the rate of extraction of individuals from a given population surpass its rate of recruitment. Several environmental and socioeconomic factors are known to act synergistically to drive human populations to reach this threshold (e.g. Bennett and Robinson 2000). Yet, the high variability across a wide spectrum of hunting scenarios also means that the probability of a game population to be overharvested will vary depending on the area in question. This high variation was evidenced, for example, in an inter-continental assessment of hunting, where no game species were estimated to be hunted unsustainably in the Amazon region as a whole, whereas around 60% of the Afrotropical game species (mostly in the Congo basin) were expected to be overharvested (Fa and Peres 2002).

Figure 3. Examples of frequently pursued South American game species (*latin name of pictured species found in parenthesis*): *a*. peccaries (*Tayassu pecari*); *b*. agoutis (*Dasyprocta prymnolopha*); *c*. trumpeters (*Psophia crepitans*); *d*. brocket-deers (*Mazama americana*); *e*. woolly monkeys (*Lagothrix cana*); *f.* spider monkeys (*Ateles chamek*); *g*. anteaters (*Myrmecophaga tridactyla*); *h*. curassows (*Crax globulosa*); *i*. guans (*Penelope superciliaris*); *j*. tapirs (*Tapirus terrestris*); *k*. howler monkeys (*Alouatta seniculus*); *l.* tinamous (*Crypturellus noctivagus*); *m*. armadillos (*Euphractus sexcinctus*); *n*. bearded-sakis (*Chiropotes satanas*). *Photos: W. Endo*

1.5. Protected Areas in South America

One of the most advocated strategies to preserve the biodiversity of a given area is the establishment of reserves where natural populations are capable of persisting in the long-term, safeguarded from potential threats more frequently observed in areas devoid of any kind of protection (Soulé 1991, Bruner et al. 2001, Chape et al. 2005, Fa et al. 2006, Le Saout et al. 2013). The creation of Protected Areas (PAs) is frequently seen as an effective strategy to aid the conservation of vulnerable populations worldwide (Chape et al. 2005, Kümpel et al 2008, Macdonald et al. 2012). This assumption has been frequently served as the basis of major conservation programs worldwide, and has been included as one of the main goals set by various United Nations intergovernmental panels, to ensure global environmental sustainability (UN 2014). With over 114,000 formally designated sites, PAs currently account for more than 19 million square kilometers of the Earth's land surface or ca. 12.9% of its area (Chape et al. 2008).

With a remarkable variety of plant and animal species, South American countries have been highlighted for their recent efforts to reduce biodiversity loss, which includes a steep expansion in the number of existing PAs (Nepstad et al. 2014). This includes multiple-use sustainable development reserves that are legally inhabited by local communities (Peres 2011). Despite a consensus on the benefits of creating and expanding PAs for *in situ* biodiversity conservation, a complex interweaving of factors are known to possibly impair the effectiveness of these areas and compromise their ability to meet proposed objectives. Proper reserve design that take into account the minimum required area to conserve target populations, a judicious and representative combination of required habitat types (Haugaasen and Peres 2005), and the connectivity among existing reserves are examples of important steps towards reaching desirable conservation goals (Ervin 2003). In Brazilian Amazonia alone, for example, more than 700,000 km^2 were recently designated as areas under protection (Soares-Filho et al. 2010), resulting in 47% of the Brazilian Amazon now being sheltered by PAs (Soares-Filho et al. 2010, Castello et al. 2013). Yet, the PA system of the country has resulted in an unbalanced coverage of its natural ecosystems. An additional cause for concern regarding Brazilian PAs is that many need to endure chronic exposure to extractive activities (Rylands and Brandon 2005). Extractive reserves, currently estimated at 67% of the total area under protection in Brazil (Rylands and Brandon 2005), are conceived to allow local human populations to exploit the resources found within these areas at varying levels of intensity. The creation of such reserves, seen as a sound way to tackle the tradeoffs between social development and nature conservation, has been a key subject of debate regarding its role to environmental conservation (Fearnside 1989, Soulé 1991, Browder 1992, Salafsky *et al.* 1993, Moegenburg and Levey 2002). The scarcity of robust empirical assessments to evaluate them, with only a few studies conducted to date and mainly focused on the impacts of selective logging (e.g. Dranzoa 1998, Azevedo-Ramos *et al.* 2006, Politi et al. 2012, Zimmerman and Kormos 2012), exposes the need of further efforts to better evaluate their effectiveness and to improve their weaknesses. Even the most restrictive PAs, however, are not guaranteed success if not properly managed. Reserve mismanagement due to various causes such as the scarcity of human and financial resources, and poor selection and accomplishment of defined strategies has been a factor contributing to their inefficacy (Higgs 1981, Ayres et al. 1991, Rodrigues et al. 2004, Gaines et al. 2010, Edgar et al. 2014).

2. Objectives

The aim of this PhD thesis was to provide a better understanding of the effects of rural human populations on medium- and large-bodied terrestrial vertebrates across distinct Neotropical sites. I was especially interested in the effects of hunting activities on game species. I also investigated the interaction between hunting activities and other activities performed by rural populations, such as fishing and cattle-raising. Since PAs are considered refuges for game populations, this thesis also tries to assess the potential effectiveness of PAs in conserving game vertebrate populations within PA boundaries.

More specifically, the study aimed to:

1. Investigate the patterns of subsistence hunting among rural populations living in the study areas (Papers I and IV).
2. Evaluate the impacts of subsistence hunting and other subsistence activities on game community structure and composition, and assess the current status of game populations in these study areas (Papers I, II, III and IV);
3. Assess the potential relationship between hunting and fishing, and its implications for conservation of game populations (Paper I);
4. Evaluate the effectiveness of protected areas in safeguarding game populations (Papers I, III and IV).

3. Thesis Structure

This doctoral thesis consists of four chapters (or peer-reviewed papers). Two chapters has been published at the time of thesis submission (Papers II and IV), one is in revision (Paper I), and one chapter will be submitted in due course (Paper III).

Paper I assesses environmental and human factors influencing the patterns of hunting and fishing by semi-subsistence rural villagers living along the middle course of the Juruá River of Western Brazilian Amazonia (Fig. 4; study sites 1 and 2). Additionally, this study evaluated the relationship between these two extractive activities and the potential implications for game management.

Paper II evaluates the influences of hunting practiced by native Amazonians (i.e. Matsigenka indigenous groups) on game community structure and composition by comparing hunted and unhunted sites within Manú National Park, Peru (Fig 4; study site 5).

Paper III describes the composition of the medium- and large-bodied mammal community found at three of the most important protected areas of the Caatinga, the largest xeric scrub and dry forest biome of South America (Fig 4; study sites 6-8). Moreover, the study evaluates the influences of rural populations living in the surroundings of these PAs and of environmental factors on the occupancy of six medium- and large-sized mammals, including four carnivore species.

Paper IV aims to better understand the current status of an important, albeit poorly studied, Near Threatened game species - the Orinoco Goose. This was done by assessing the species occupancy patterns within the study area (Fig 4; study sites 1-4), related to both environmental and human variables. The impacts of human populations on the species was also assessed by monitoring the species offtake by local hunters.

4. Methods

4.1. Study Area

The studies included in this thesis were conducted at eight distinct South American protected areas of different denominations (Fig. 4). Five of these PAs were located within the Amazon biome, with four of them located in the Brazilian State of Amazonas and within the Juruá basin (Papers I and IV): the 253,227 ha federally-managed Médio-Juruá Extractive Reserve (Fig 4; study site 1); the 632,949 ha state-managed Uacari Sustainable Development Reserve (Fig 4; study site 2); the 1,531,300 ha Deni Indigenous Territory (Fig 4; study site 3); and the 596,433 ha Kanamari do Xeruã Indigenous Territory (Fig 4; study site 4). The fifth Amazonian PA was the 1,716,300-ha Manú National Park (Paper II; Fig 4, study site 5), in the Peruvian region of Madre de Dios. The three remaining PAs (Paper III) were all PAs managed by a federal government agency and placed within the Brazilian *Caatinga* biome: the 91,849 ha Serra da Capivara National Park (Fig 4; study site 6), in the Piauí State; the 104,843 ha Raso da Catarina Ecological Station (Fig 4; study site 7); and the 11,216 ha Contendas do Sincorá National Forest (Fig 4; study site 8), with the two last PAs found in the Brazilian state of Bahia.

Figure 4. Map depicting the eight protected areas where the studies were conducted: 1. Médio-Juruá Extractive Reserve; 2. Uacari Sustainable Development Reserve; 3. Deni Indigenous Territory; 4. Kanamari do Xeruã Indigenous Territory; 5. Manú National Park, 6. Serra da Capivara National Park; 7. Raso da Catarina Ecological Station; 8. Contendas do Sincorá National Forest .

4.2. Data Collection

The thesis relied on three distinct methods to estimate game population parameters in the study areas: line-transect censuses, camera-trapping and censuses along rivers.

Line transect censuses were conducted at Manu National Park (Paper II) in seven distinct locations within the reserve, and summing a total of 20 transects. Surveyed sites placed 15-70 km away from Matsigenka settlements were considered sites with no direct influence of hunting activities practiced by local indigenous groups. Censuses were conducted along transects following methodological guidelines provided by Peres and Cunha (2011).

Camera-trapping surveys were carried out at the three distinct PAs representing the Caatinga biome (Figure II; Paper III) and comprised a total of 89 camera-trap stations established across the survey sites (SCNP = 41, RCES = 23,CSNF = 25).

To study the Orinoco Goose population occurring in the middle portion of the Juruá river (Paper IV) we conducted an extensive survey effort based on visual censuses along the Juruá river and its tributaries, using motorized boats and at least two observers equipped with binoculars.

In addition, daily offtake of game meat extracted by rural human populations along the Juruá region was assessed, and the data collected were used in two studies included in the thesis (Paper I and IV). These data were obtained by surveying local villages and conducting structured interviews on a weekly basis during the study period. A total of 222 households from 28 villages were surveyed for 44 months. At each of the surveyed villages one or more local assistants were trained to carry out household surveys. Additionally, fish offtake was also assessed during these interviews to be used in the study (Paper I).

All studies assessed, by different approaches, the influences of human populations on game populations. In all chapters, possible changes in game population parameters related to the distance from human populations were assessed, including villages, urban centres and populated areas surrounding the PAs. Human influences were also assessed by investigating potential differences in areas with differing use restrictions (Paper III and IV).

Environmental variables were represented by data extracted from satellite imagery (Paper I, III and IV), and *in situ* habitat type assessments (Paper III and IV).

4.3. Data Analysis

In all papers, the data collected were modelled in order to investigate potential relationships among selected variables and to predict parameter values.

In Paper I and III the relationship between response variables (game and fishing yield and catch per unit effort (CPUE); *Neochen jubata* encounter rate) and selected predictors were modeled by building linear models that incorporated random parameters. Mixed models have the advantage of accounting for pseudoreplication and minimizing the use of degrees of freedom, thereby increasing predictive power. These models were also able to have a hierarchical structure by nesting variables across spatial scales.

In Paper II, the best fit models that were able to explain the distribution of perpendicular distances of every animal detected during the census were selected, thereby, providing estimates of population densities for most surveyed species at each surveyed site. Best-fit models were selected by choosing those with the lowest Akaike Information Criteria values, a balance between predictability power and lower number of parameters (Buckland et al. 1993). For species where the number of detections were insufficient ($n<39$) we relied exclusively on encounter rates, here defined as the number of individuals (or groups) encountered per 10 km walked. Aggregate game community biomass estimates were derived using the species population densities obtained in this study and average body mass values of each species found elsewhere (Ohl-Schacherer et al. 2007, Peres 1999 and Terborgh et al. 1990).

In Paper III, we conducted occupancy models to investigate the relationship between selected predictors and the species occupancies. Occupancy models were used to estimate species occupancy probabilities at each surveyed site (camera-trap station). Occupancy models, as well as distance sampling models, are capable of dealing with incomplete detections, such as those obtained with camera-trap surveys and line-transect censuses.

Multi-model inference procedures are a powerful tool to assess the ability of selected parameters included in study models (Bunham and Anderson 2003). This procedure was used in Paper II, IV and V.

Apart from the different modeling techniques used in the studies, a few other statistical procedures were also used to investigate potential patterns in our results. The detection of all sites were considered similar, since the tests performed using Analysis of Variance (ANOVA) were not significantly different across sites, allowing us to pool the perpendicular distance values across all census sites. Constrained correspondence analysis (CCA) was also performed in Paper III.

5. Results and Discussion

5.1. *Current status of game populations*

Paper II presents one of the highest aggregate game vertebrate biomass ever reported in Amazonia. The study revealed high population densities for some of the most pursued and vulnerable game species found in Neotropical forests, including spider monkeys (*Ateles*), woolly monkeys (*Lagothrix*) and white-lipped peccaries (*Tayassu pecari*). These results confirm the high importance of Manú National Park as an important haven for Amazonian wildlife, with healthy game communities, particularly in sites farther from local Matsigenka indigenous villages.

Paper III provides one of the first assessments for the medium to large-bodied mammal community structure and composition occurring in the Brazilian Caatinga biome. This study, conducted in some of the most important PAs of this biome, indicates that the extant meso- and mega-fauna has been impoverished, whereby a number of important Caatinga species are either absent or occurring at very low densities. This includes once common and widespread game species, such as the giant anteaters, peccaries and jaguars.

Paper IV describes what is likely to be the largest Orinoco goose population ever reported for the Amazon region, with hundreds of individuals inhabiting the middle course of the Juruá River. The species, however, was shown to be largely restricted to the meandering sand belts formed along the margins of the main river, with only a few individuals observed in the surveyed tributaries. The study, disclosing a previously overlooked population and suggesting high habitat specificity, provides information of high relevance to the species conservation, currently listed as Near Threatened by the IUCN (BirdLife International 2012).

5.2. Influences of hunting and other human activities on game populations.

The patterns of hunting and fishing activities conducted by semi-subsistence Amazon forest dwellers, and their relation with environmental and human variables were assessed in Paper I. The study suggests that the seasonal flood pulse affects game and fish exploitation patterns. Periods of high river water level were periods of lower fish yield and game and fish CPUE, whereas the same period resulted in higher game yield. The study showed a strong interconnection between both extractive activities, with important implications for game management.

Paper II provides important insights on the influence of traditional Matsigenka subsistence "bow-and-arrow" hunters on the game populations of Manú National Park. Despite the subsistence nature of the Matsigenka hunting activities and the low efficiency of their hunting gear (Alvard 1995), the areas under direct influence of hunting by local indigenous populations presented game communities considerably distinct in their structure and composition to those found in unhunted areas within the reserve. Aggregate game vertebrate biomass in hunted sites, for example, was 2- to 4-fold lower than those obtained for unhunted sites with similar forest type (upland terra firme forests). As expected, harvest-sensitive game species (e.g. large-bodied ateline primates) were those presenting the largest differences between hunted and unhunted sites. In contrast, species known to be more resilient to hunting did not show any clear differences (e.g. red brocket deer) or were in fact more abundant (e.g. Spix's guan) in hunted sites than in unhunted sites.

The study in the Caatinga biome (Paper III) also provides strong evidence for effects of humans on medium to large-bodied vertebrates. The occupancy of 4 out of the 6 species analyzed was strongly related to the predictors used as proxies of human influence, namely the frequency of cattle records and the distance to the PA border. The species showed a negative relation of occupancy with an increase in cattle presence and with a decrease in the distance to the PA border. Again, the species known to be less sensitive to hunting and other human activities were the ones with occupancies being only weakly affected negatively by these variables (crab-eating fox) or even positively affected by them (black-rumped agouti).

Paper IV shows a steep decrease in the Orinoco goose encounter rate with the proximity of both urban areas and human population density, underlining the negative effects of local human populations on the species. The low rate of goose killings by local villages suggests that the bird is a non-preferred game species in the study area. However, because the species uses the sand belts along the main river channel and thus remain exposed to hunters, it is imperative to create stronger measures to protect the species in this type of ecosystem.

5.3. Effectiveness of current protected areas for game conservation

Overall, the thesis presents evidence that the surveyed sites still harbour important populations of medium to large-bodied land vertebrates, and therefore confirms that PAs are important for conservation purposes. However, the same results show that human populations inside or nearby these areas significantly affect local game populations and, ultimately, the game community structure and composition of these areas, even at varying levels of harvest intensity. Because these results refer to PAs with considerably lower human densities than what can be usually seen across South America and elsewhere in the tropics, this work underlines the crucial importance of further studies of human impacts on game populations to better conserve these species.

Despite evidence of human influences on the surveyed game communities, the results also show that the core areas of these PAs, further removed from human populations, are able to better sustain the game populations.

The thesis also tries to assess whether an increasing degree of protection improves the conservation status of local game populations. The results, however, seem to have produced divergent conclusions. The study in the Juruá region (Paper IV) showed that Orinoco geese more frequently occupied beaches with the highest protections status (turtle nesting beaches or *tabuleiros*) than beaches with more relaxed resource extraction rules. On the other hand, the most restrictive PA surveyed in the Caatinga (Raso da Catarina Ecological Station) shows the highest presence of cattle, concomitantly with lower levels of occupancy for species important for conservation. This contrasts with results obtained in Serra da Capivara National Park, a PA with lower restriction rules. Although several factors may affect the occupancy of the surveyed species, including environmental variables, I believe that the heavy presence of cattle inside Raso da Catarina Ecological Station is a clear example of the low efficiency in the application of protection rules that undermines wildlife protection in many PAs across the South American continent.

5.4. Seasonal patterns of game extraction

Paper I provides a clear example of how seasonal environmental changes may affect human and animal populations. The rise of the waters of the Juruá River was strongly related to a decline in fish yield and CPUE, and a rise in game yield, despite a decrease in game CPUE values. In addition, Paper IV shows a seasonal variation in Orinoco goose occurrence in the Middle Juruá region. As their beach habitats become flooded in the high-water season, the species disappear from the region, suggesting a migratory behaviour later confirmed by other studies (L. Davenport et al., unpub. data). Their permanence in the region therefore appears to be constrained by the rising of the waters and the consequent temporary absence of their preferred habitats. This game species is thus unavailable to hunters for large parts of the year.

6. Concluding Remarks and Future Perspectives

This thesis provides important insights regarding the influences of rural populations — living within or in the vicinity of South American PAs — on game populations. The results clearly show that even remote sites with low human population densities can be affected to a point where significant changes on medium to large-bodied vertebrate populations can be detected. Moreover, the results also evidenced the pervasiveness of protected areas to human influences, calling attention to the need of further assessments of human influences on such game populations.

Another important insight provided by the studies herein is the potential interaction of different human activities and game extraction, suggesting the need to conduct a more transversal assessment of rural livelihoods when designing wildlife conservation strategies. Fishing and cattle husbandry were two activities embedded within the livelihoods of surveyed populations that are likely to be, directly or indirectly, promoting declines in the abundance of game populations. I therefore advocate further studies that may refine our understanding on how these activities affect land vertebrates.

The existence of well-defined and pronounced changes in subsistence hunting and the spatial occupancy patterns of species along the year, particularly related to the pulse of inundation of surveyed sites along the Juruá River, also underlines the importance of discriminating seasonal cycles when managing exploited populations.

Finally, the results show that differences in levels of natural resource use restriction are also important to increase the effectiveness of species conservation. These rules, however, need to be carefully and continuously assessed and maintained in order to be effective.

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8. Other Publications

1. Nichols,E.; Uriarte, M.; Peres, C. A., Louzada, J.; Braga, R. F.; Schiffler, G.; Endo, W.; Spector, S. H. 2013. Human-induced trophic cascades along the fecal detritus pathway. *PloS ONE* 8(10): e75819.
2. Newton, P.; Nichols, E., Endo, W.; Peres, C. A. 2012. Consequences of actor level livelihood heterogeneity for additionality in a tropical forest payment for environmental services programme with an undifferentiated reward structure. *Global Environmental Change* 22(1): 127-136.
3. Palminteri, S.; Powell, G.; Endo, W.; Peres, C. A. 2011. Usefulness of species range polygons for predicting local primate occurrences in southeastern Peru. *American Journal of Primatology* 73(1): 53-61
4. Newton, P.; Endo, W.; Peres, C. A. 2011. Determinants of livelihood strategy variation in two extractive reserves in Amazonian flooded and unflooded forests. *Environmental Conservation* 39(2): 97-110.
5. Endo, W.; Peres, C. A.; Rebelo, G. H.; Baniwa, E.; Shepard, G. H.; Mesquita, R. C. G. 2010. Padrões de uso da vida silvestre pelos índios Baniwa e considerações sobre a sustentabilidade da caça no Médio Rio Içana. In: Cabalzar, A. (org.) *Manejo do Mundo - Conhecimentos e Práticas dos Povos Indígenas do Rio Negro*. Instituto Socio Ambiental/FOIRN
6. Haugaasen, T.; Endo, W.; Maira, L. L.; Peres, C. A. 2013. Red-billed Ground Cuckoo *Neomorphus pucheranii lepidophanes*. *Neotropical Birding* 12: 55-56.
7. Davenport, L.; Endo, W.; Kriese, K. 2013. Orinoco Goose (*Neochen jubata*), *Neotropical Birds Online* (T. S. Schulenberg, Editor).

PAPER I

Paper I assesses environmental and human factors influencing the patterns of hunting and fishing by semi-subsistence rural villagers living along the middle course of the Juruá River of Western Brazilian Amazonia. Additionally, this study evaluates the relationship between these two extractive activities and the potential implications for game management.

Photo: W. Endo

Seasonal variation in animal protein acquisition by semi-subsistence Amazonians in floodplain settlements

Running Head: protein acquisition by rural Amazonians

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Biological Conservation, in revision

ABSTRACT

Rural populations frequently rely on game vertebrates and fish to supply their daily protein requirements. However, few studies have tried to assess the factors driving hunting and fishing activities and the potential relationship between these extractive activities. In this study, we assessed game and fish extraction by 222 semi-subsistence households from 28 villages in the lowland Brazilian Amazon. The study shows that rural settlements along major white-water tributaries of the Amazon rely heavily on game and fish resources. During the 44 months study, a total of 32 114 kg of game and 261 752 kg of fish were harvested , translating to an average extraction of 30.5 ± 109.9 g person^{-1} day^{-1} and 1,519.4 ± 1,037.6 g person^{-1} day^{-1} for game and fish, respectively. While 97.93 ± 0.03% of all fishing trips resulted in fish catches, only 77.12 ± 27.02% of the hunting forays successfully obtained at least one forest vertebrate. The flood pulse had a strong effect on both fishing and hunting activities. However, while fish yield and catch per unit effort (CPUE) was negatively affected by rising river waters, game yield was inversely related to the same variable. Game yield was also an important variable explaining fish yield, indicating a strong compensatory interaction between these protein procurement activities. The results highlight the importance of considering both activities when planning conservation and management of land vertebrates and aquatic organisms.

Keywords: hunting, fishing, Amazonia, flood pulse, várzea

Highlights

- We assessed the drivers of fish and game extraction by semi-subsistence Amazonians.
- The flood pulse had a strong effect on both fishing and hunting activities.
- Fish yield and CPUE were negatively influenced by the rise of the river water.
- Game yield was also a strong predictor of fish yield.
- Results suggest that both activities must be addressed when planning conservation actions.

1. Introduction

Terrestrial game vertebrates and fish are central to the nutritional livelihoods of a large number of rural people, particularly in remote tropical forest regions where access to farmed plant protein and livestock are limited (Fa et al. 2002; Sirén & Machoa 2008; Parry et al. 2010; Golden et al. 2011). The heavy reliance of rural semi-subsistence communities in the tropics on wild animal protein and fat makes the sustainability of fishing and hunting activities a cause of great concern for conservation, food security and social welfare agencies (Davies 2002; Ceballos & Ehrlich 2010; Brashares et al. 2014; Dirzo et al. 2014; Parry et al. 2014).

In Amazonia, the dietary importance of vertebrate populations to human populations is exacerbated by the poor protein content of food crops typically cultivated in this region (e.g. manioc and plantain; Vasey 1979; Roosevelt 1980), fomenting an annual consumption of a minimum of 89.2 tonnes of wild meat by local communities in Brazilian Amazonia alone (Peres 2000). Despite recent efforts by governmental and non-governmental agencies to minimize impacts of human activities on natural areas (Nepstad et al. 2014; Tollefson 2015), policies and management guidelines for wildlife extraction are still at their infancy in the Amazon and further studies are needed in order to design evidence-based conservation strategies. Moreover, the relentless human population growth and conversion or degradation of natural forest habitats currently seen in tropical forest regions (Trancoso et al. 2010; Davidson et al. 2012; Castello et al. 2013; Espinosa et al. 2014) are likely to compromise current levels of fish and game consumption, as well as the long-term persistence of overexploited vertebrate populations.

Lowland Amazonia spans an area of 4.2 million km^2 ($\leq$300m asl) across nine countries and is comprised of a vast mosaic of ecosystems. Despite the existing plethora of different habitats, Lowland Amazonian forests are roughly distinguished by two broad types with distinct floristic and faunal composition (e.g. Peres 1997; Haugaasen & Peres 2005a, b; 2006, Bobrowiec et al. 2014): unflooded forests (hereafter termed "terra firme") above the maximum flood level of Amazonian rivers, and seasonally flooded forests subject to seasonal flooding. Seasonally flooded forests along major rivers may experience an inundation period of up to six months each year, as river water level fluctuations may reach 15m in amplitude (Goulding et al. 2003). This dramatic flood pulse clearly affects the distribution and seasonal dynamics of both terrestrial and aquatic organisms (Bodmer 1990; Fernandes 2006; Haugaasen & Peres 2007; Beja et al. 2010).

Seasonal changes in landscape structure may provide challenges to local human populations in terms of access to different food resources. For example, the prolonged annual flood pulse results in the spatial dispersion of fish across vast floodplains that may extend tens of kilometers from the main river channel (Goulding et al. 2003). Consequently, semi-subsistence Amazonians settled along major rivers must alter their foraging strategy and effort in response to such climatic and hydrological events, or shift their exploitation activities to alternative targets. A decline in fish density, therefore, is expected to lead human foragers to focus on terrestrial game populations more intensively as fishing yields per unit of foraging effort decline substantially. This is consistent with a study in West Africa, where noticeable shifts in offtake and consumption from fish to bushmeat coincide with periodic shortages of marine and freshwater fish stocks (Brashares et al. 2004). However, this pattern of seasonal alternation between terrestrial and aquatic sources of animal protein is yet to be comprehensively assessed in an Amazonian setting. Several studies have described the patterns of fishing and hunting activities conducted by rural Amazonians (e.g. Nietschmann 1972; Behrens 1981; Stocks 1983; Kaplan & Kopischke 1992; Pezzuti & Chaves 2009; Endo et al. 2010), but do not consider the drivers of vertebrate prey consumption or the potential inter-relation between these two important subsistence activities. This is a crucial wildlife conservation and food security issue, because animal protein intake by local communities is inherently compensatory on a per capita basis across prey species within the same or different environments. In other words, eventual depletion of a given protein source is likely to lead human populations to rely on alternative sources of protein so that an emphasis on fishery exploitation in freshwater settings can alleviate local demand on equivalent protein sourced from terrestrial vertebrate species hunted in forest environments and *vice versa*.

Here we examine natural resource use by human populations in the lowland Amazon by providing a large-scale assessment of patterns of fish and game extractive activities in the Juruá river basin, Brazil. Specifically, we investigate the environmental and socio-economic covariates that may affect such activities, and the potential inter-relation between fishing and hunting activities in this region. Finally, we discuss implications of these findings for the long-term sustainability of wildlife resource extraction in a pan-Amazonian context.

2. Material and Methods

2.1 Study Area

The study was conducted along a ~400-km section of the middle third of the Juruá River, in the western Brazilian Amazon (Figure 1). This area includes two major sustainable-use protected areas: the federally managed 253 227 ha Médio Juruá Extractive Reserve, and the state managed 632 949 ha Uacarí Sustainable Development Reserve. These reserves combined are home to ~4,000 semi-subsistence people who exploit natural resources, including fish and other aquatic prey, game vertebrates and non-timber forest products. A large proportion of their carbohydrate staple diet is based on manioc, which is cultivated by virtually every resident family (Newton et al. 2011). Additionally, the area encompasses the urban center of Carauari. This town is located 60 km from the border of the Uacarí Sustainable Development Reserve, and is inhabited by approximately 19 700 people (IBGE 2011). Our study area encompassed a fluvial distance from Carauari of 392 km, thereby setting a strong human population density gradient.

The region has a wet tropical climate (mean temperature = 27.1ºC) and a well-defined rainfall regime, with the rainiest period from December to May. Mean annual rainfall is 3 679mm (2008-2010; Bauana Field Station; S 5º26’19’’, W 67º17’12’’). Terra firme and seasonally flooded várzea forest are the two main forest types in the region, the former comprising 78% of the study area (Hawes et al. 2012). Várzea forest is a type of floodplain forest that occurs along white-water rivers of Andean or pre-Andean origin, and are exceptionally productive due to the annual deposition of nutrient-rich sediments brought by the floodwaters (Junk 1984). Várzea forests in the study region are subjected to an annual flood pulse of around 12m in amplitude (Figure S1), although the inundation period varies with topography. Mean monthly values of river discharge range from 135 to 1,407 m^3/sec (1973-2010; Porto do Gavião; Petrobrás S.A.) and January-May is the period with highest water discharge.

2.2 Household surveys

We monitored game and fish yields of 222 households from 28 villages across the study area (Figure 1). Villages had a mean number of 58.4 ± 44.5 inhabitants (mean±SD) and households contained 5.7 ± 1.86 members including children (source: CEUC-SDS, ICMBio). Resource use monitoring consisted of structured interviews using questionnaires, conducted once weekly by previously trained local assistants living in each of the monitored villages. We interviewed 7.6 ± 3.8 (mean±SD) households per village. These interviews were conducted in each household during the entire survey period lasting from April 2007 to August 2010.

During weekly interviews, respondents were asked to provide details of each protein acquisition foray conducted over the last two and seven consecutive days for fishing and hunting trips, respectively. Based on information collected during previous visits at the study area, fishing was known to be more frequently practiced than hunting so data from memory recalls had to be restricted to only 2 days to avoid omission and commission reporting errors. Data collected included the number of individuals of each species captured (if any), date, and the start and end times of each trip. Game and fish offtake brought to the villages were weighed and identified by the field assistants whenever possible using a set of multiple scales from 1kg to 50kg. Due to the large amount of fish brought to the villages, a considerable percentage of the fish were not weighed. Yet, since fish trade is common practice in most villages and fish are valued according to their weight (with larger-bodied fish returning higher prices), information on fish weight was successfully obtained during interviews and considered a reliable source of data for estimates of fish biomass yield from each village. Furthermore, additional data on body mass from direct field measurements or information found in the literature were compiled to augment the robustness of weight records for species yielding small sample sizes.

2.3 Predictors of Protein Acquisition by rural Amazon populations

To assess the influence of inundation on fishing and hunting activities we used a classification of areas subjected to different inundation regimes based on multi-temporal (2006-2011) remote sensing data of the study area. These data were obtained by the Advanced Land Observing Satellite (ALOS) Phased Array type L-band Synthetic Aperture Radar sensor (PALSAR) system, using a 100-m spatial resolution (see Hawes et al. 2012). Synthetic aperture radar (SAR) sensors are able to generate appropriate data sets to map flooded forests, due to its ability to overcome problems of forest canopy cover, atmospheric and illumination conditions, and provide reliable measurements of the flood extent in wetland habitats (Arnesen et al. 2013). Based on a time series of 12 different ScanSAR scenes, a total of seven different forest categories were distinguished for this study: unflooded forests, permanent water habitats, and várzea forests with the following mean flooding periods: <1 month/year, 1-2 months/year, 3-5 months/year, 6-8 months/year, 9-12 months/year.

Based on the classified imagery, we were able to create distinct environmental predictors to be used in the analyses. As a measure of the flood persistence we created an index (FP) that included the contribution of each floodplain habitat, using the following equation:

$$FP = \sum VZ_i * FL_i$$

Where VZ is the percentage of the area covered by each habitat category within a 10-km radius buffer around each surveyed village, and FL is the mean number of months each area remained inundated.

To represent the availability of open wetland habitats, such as oxbow lakes, to local human populations and assess the potential influences of these habitats on the patterns of fish and game extraction a second environmental variable based on the ScanSAR images classification was created, considering the percentage of these habitats within each selected buffer. The total area of each habitat category occurring within each buffer was calculated using ArcGIS (ver.10.0) and Global Mapper (ver. 9).

To evaluate the effect size of the seasonal flood pulse on fishing and hunting yield, the mean monthly water discharge (m^3/sec) of the Juruá river, based on daily readings over a 38-year period (years: 1973-2010; Porto do Gavião; Petrobras S. A.), was also used as a covariate.

As a proxy for protein demand on fish and forest vertebrates, we calculated the human population density (HPD) within each village and its surrounding area. This was done by summing the total number of inhabitants settled within a 10-km radius around each monitored village. Additionally, to investigate the potential influence of proximity to urban markets on fish and game yields, we measured the Euclidean distance of each village to the urban center of Carauari by using satellite images of the study area.

2.4. Data analysis

Month-averaged daily rate of fish or game biomass acquired in all monitored households was used as the response variable to assess patterns of fish and game harvest. Additionally, to assess the direct influence of hunting on fishing activities, fish yield was also modelled with the inclusion of game yield as an additional fixed parameter. For this modelling, we used non-averaged values from a subset of the fishing and hunting dataset, exclusively containing days for which data for both fishing and hunting were available.

The daily rate of fish or game biomass acquired in all monitored households was used as the response variable to assess patterns of fish and game harvest. To relate the variation in fish and game catch per unit effort (hereafter, CPUE) to the explanatory variables, we calculated the amount of game or fish biomass obtained by villagers divided by the time interval allocated to each fishing or hunting foray (expressed as kg h^{-1}). Fish CPUE was obtained from only eight villages and these were, therefore, the only villages included in these analyses. A small proportion of fish captures (<0.01 %) were excluded from the analyses because the fish species identity was either ambiguous or unavailable.

We performed Linear Mixed Models (LMMs) using a Gaussian error structure to assess the relationship between all the selected covariates (river water level, distance to the urban center, proportion of the area consisting of open wetlands, and human population density) and the variation in both total yield and CPUE of fish and game. Surveyed households were nested within villages, so the latter was used as a random variable to account for the non-independence of surveys conducted across all sites. Additionally, because each household was surveyed during different months, we considered river water level as a repeated measure and included it as a random parameter in the model structure.

A multimodel inference approach was used to obtain the most parsimonious models from all possible first order candidate subsets of the global models. Comparisons of candidate models were done using Maximum Likelihood (ML) procedures. This is more appropriate than Restricted Maximum Likelihood (RML) to compare model subsets with variable fixed parameter structures (Zuur *et al.* 2009). The LMMs and multimodel inferences were performed using the lme4 (Bates et al. 2013) and MuMIn (Bartón 2013) in R version 3.0.2 (R Core Team 2013). These procedures allowed us to rank the most parsimonious models, evaluate the contribution of each parameter to the set of top models ($\Sigma w \leq 0.95$), and predict the coefficients for each parameter through model-averaging procedures.

The flood persistence (FD) index and open wetland area were strongly correlated (Pearson's product moment correlation; $r = 0.78$, $P < 0.001$) so open wetland area was selected as the best variable to represent the availability of aquatic habitat in the models. All remaining selected predictors were only weakly correlated (mean ± SD Pearson correlations = 0.20 ± 0.16, range = 0.01-0.62; $P<0.05$ in 6 of 48 correlations) and were thus included as covariates in the global models.

Results are expressed as mean ± SD, unless otherwise specified.

3. Results

Our results are based on an effort of 42 384 and 151 431 survey-days of fishing and hunting activities, respectively, over the 44 months of study. Of these, 28 668 (67.6%) reported fish yields but only 1,274 (0.84%) reported game yields. In total, 2,375 mammals, birds and reptiles were killed during all hunting forays, whereas an estimate of 226 528 fishes were captured during all reported fishing trips, suggesting that fish is a more important source of protein in the surveyed villages. This amounts to an estimated 32 114 kg of game and 261 742 kg of fish harvested during the entire study period, with villagers extracting an average of 1,519.4 ± 1,037.6 g $person^{-1}$ day^{-1} and 30.5 ± 109.9 g $person^{-1}$ day^{-1} for fish and game vertebrates, respectively.

An average of 97.93 ± 0.03% of all fishing trips resulted in fish catches, whereas only 77.12 ± 27.02% of the hunting forays successfully obtained at least one forest vertebrate. Hunting, however, was a protein acquisition activity 3.5 fold more time-efficient than fishing, providing a mean CPUE over all hunting forays of 8.41 ± 15.51 kg h^{-1}, whereas fishing resulted in a mean CPUE of 2.00 ± 1.39 kg h^{-1}.

3.1 Fish yield and CPUE

No best single models were able to consistently explain the variation in fish extraction (Table 1, Table S1(a,b)). The set of most parsimonious candidate models, representing a 95% probability of including the best model, consisted of three distinct models explaining fish yield and five distinct models explaining changes in fish CPUE (Table 1, Table S1(b)).

River water discharge was the most important variable explaining the variation in fish yield and fish CPUE. This variable was retained in every top-ranked candidate model and was positively related with both response variables (Table 1, Fig. 2(i,j), Table S1(a,b)), clearly showing the strong influence of the flood pulse on fishing activities.

Both response variables responded positively to an increase in the proportion of open wetland area and distance to the urban center (Table 1, Fig. 2.(a,b,e,f), Table S1(a,b)). Conversely, human population density had a strong negative effect on fish yield, but only a weak effect on fish CPUE (Table 1, Table S1(a,b)).

Results from the fish yield modelling incorporating game yield as an additional fixed parameter in the global model showed a strong negative effect of game yield on fish yield values (Table S1(e)), which we assume to be compensatory at least at a household scale. All other parameters presented similar coefficients to those obtained when modelling fish yield using the entire fishing dataset (Table 1, Table S1(a)).

3.2 Game yield and CPUE

More than one potential candidate model was able to explain the variation in game extraction (Table 1, Table S1(c,d)). The set of best candidate models for game yield encompassed six distinct models, while the set of most parsimonious models for game CPUE consisted of nine distinct models (Table 1, Table S1(c,d)).

Following the same patterns found for fish yield, river water discharge was the only covariate retained in the entire set of top-ranked candidate models explaining the variation in game yield, presenting a strong positive effect on this response variable (Table 1, Fig. 2(k), Table S1(c)). This clearly indicates that villagers were more likely to go hunting when river water level was high, and fish stocks diluted across the vast inundated floodplain. The variation in hunting CPUE (kg h^{-1}) was also consistently explained by distance from the urban center, being positively related to this covariate (Table 1, Fig. 2(h), Table S1(d)). Game CPUE was also strongly and positively related to river water discharge (Table 1, Table S1(d)). The two other variables, proportion of open wetland and human population density, were poorly related to both game yield and hunting CPUE (Table 1, Figure 2(d), Table S1(c,d)).

4. Discussion

4.1. Fish and Game Yields

As a resounding endorsement of the aquatic productivity of major white-water tributaries of the Amazon, protein extractivists along the Juruá River consistently kept fish yields well above those obtained for game, independently of the period of the year. The low frequency of hunting forays compared to fishing trips conducted by the surveyed extractors across the study area, suggests that hunting is an activity of secondary importance to human populations living within or nearby floodplain areas in the Amazon. This pattern is similar to other Amazonian sites, such as the Mamirauá Sustainable Development Reserve in the lower Japurá River, where local populations are known to rely on fish to obtain around 80% of their daily protein intake (Henderson & Crampton 1997).

Our study clearly shows higher game CPUE values than those obtained for fish. However, the consistently greater proportion of successful fishing trips that were able to provide some energetic return compared to hunting forays show that fishing is as a steadier and more reliable food acquisition strategy, leading local floodplain dwellers to rely on this activity as a primary source of protein. Poor hunting success has also been reported for other tropical forests, with failure rates of up to 68% of all hunting forays (Wadley et al. 1997; Gragson 1992), implying that this may be a common pattern in such regions. This is likely to be a preponderant factor driving rural populations to favor fishing over hunting. Yet, several other factors may also contribute to a higher preference for fishing. These include the engagement of villagers in the fishing trade, the use of less energetically costly means of transportation and prey capture during fishing activities (e.g. motorized canoes and fishing nets), risk avoidance (e.g. snake bites while walking in the forest), or even dietary or cultural preferences and physiological constraints (see Speth & Spielmann 1983; Milton et al. 1991; Malainey et al 2001).

4.2. Interplay between Hunting and Fishing

Supporting the hypothesis of a reciprocal influence of hunting and fishing activities, our results portray a decrease in hunting with the intensification of fishing and *vice versa*. Game yields had also a strong effect on fish yields when included as one of the predictors in the fish yield models (Table S1(e)), indicating a strong compensatory interaction between these protein procurement activities. One potential explanation for such relationship may be the inability of extractors to concomitantly conduct both activities. This constraint is likely to force extractors to rely on a single activity over other potential extractive activities. This relationship may be less evident if not assessed at the individual level, as collective groups may have different extractors simultaneously exploiting distinct protein sources. Nevertheless, our results suggest that this mutually exclusive relationship is strong enough to be detected even when analyzed at the household level.

Fish CPUE and fishing yields responded negatively to an increase in river water discharge (Table 1, Fig. 2(i,j), Table S1(a,b)). Periods of high river water level are characterized by the expansion of suitable habitats to aquatic organisms. This facilitates fish dispersion, thereby greatly reducing fish density per unit area (Fernandes 2006). Conversely, fish stocks become concentrated during periods of low water level. Because large terrestrial vertebrates are almost invariably one of the major sources of protein exploited in tropical forests (Fa et al. 2002, Milner-Gulland et al. 2003) it is reasonable to expect that a lower fish availability will cause a higher capture effort of land vertebrates by semi-subsistence Amazonians. Indeed, results showed an increase in game yields during the floodplain inundation season (Table 1, Fig. 2(k), Table S1(c)), confirming a higher reliance on game during periods of lower fish availability. This is also corroborated by the fact that game CPUE responded negatively to an increase in river water discharge (Table 1, Fig. 2(l), Table S1(d)). This observed trend cannot be attributed to a higher seasonal availability of game during this period leading human populations to opportunistically increase their game yields.

Amazonian fishermen and fisherwomen modify their patterns of resource exploitation along the year in order to mitigate the impacts of seasonal environmental changes on their fish consumption levels. This includes the exploitation of different sites and the use of a wide range of fishing techniques (Cerdeira & Ruffino 2000). In addition, the migratory behavior of several fish species is likely to partially counterbalance the seasonal decline in the availability of other fish species (Junk et al. 1997; Araújo-Lima & Ruffino 2003), allowing fisherfolk communities to switch their diets to other taxa more easily captured at this time. Indeed, Newton *et al.* (2011) uncovered well-defined seasonal changes in yield rates of specific fish taxa in the study area. However, our results indicate that these strategies may, at best, only partially deal with the constraints imposed by the limited access to fish during peak flood pulses.

Both fish and game CPUE values were strongly and positively influenced by an increase in distance from the urban center (Table 1, Fig. 2(e,g), Table S1(b,d)), likely indicating a greater abundance of both fish and game stocks in areas far from large human conglomerates. Yet, despite the consistent increase in fish yields related to this variable, this effect was not significantly strong for game yields. These patterns corroborate the routine reliance of extractors living in Amazonian floodplain forest sites for fishing stocks rather than forest wildlife, especially in areas with a higher fish productivity, thereby relieving hunting pressure on game populations.

The dietary profile of forest dwellers is also expected to be influenced by environmental features of the landscape (Milton et al. 1991). Our results show that open wetland habitats are important for rural populations in the Amazon, as they are linked to higher fish CPUE and yield. Open wetland habitats in the Amazon, particularly oxbow lakes, are highly valued by both local communities and commercial fishing boats as prime fishing areas, often leading to conflicts between these stakeholders (McGrath et al. 1993). Commercially valuable Amazonian fish species, such as arapaima (*Arapaima* spp.) and tambaqui (*Colossoma macropomum*), are commonly found in these habitats, where they are intensively pursued (Isaac & Ruffino 1996; Castello *et al.* 2009), including our study area.

Despite the strong effect of open wetland habitats on fishing, hunting patterns were not consistently affected by the same variable. Hence, this does not explicitly demonstrate a decrease in hunting activities concomitant with an intensification of fishing in sites with a higher proportion of wetland habitats. It is possible that other factors related to this variable may counterbalance the otherwise expected decline in hunting activities. The weaker dichotomy between terrestrial and aquatic environments, for example, with high-water floodplain forests being frequently used for both fishing and hunting activities targeting arboreal taxa, such as howler monkeys, may allow the costs of unsuccessful hunting forays to be compensated by the capture of fish in such areas. Furthermore, because floodplain forests are also frequently accessed by dugout canoes rather than on foot, it is possible that the potentially low energetic costs involved may be an additional motivation for hunters in such areas.

4.3. Implications for Wildlife Management

The clear association between fishing and hunting activities indicates that potential declines of fish populations due to overharvesting are likely to be accompanied by hunting intensification in fish depleted areas. Freshwater fish species of subsistence value in western Amazonia typically have high reproductive rates (e.g. Lowe-McConnel 1987; King & McFarlane 2003) and are generally assumed to be more resilient to human exploitation than populations of forest vertebrates (Stearman 2000). Moreover, standing biomass of fish is usually many orders of magnitude greater than that of terrestrial mammals in the Amazon (Gragson 1992), suggesting that exploited fish stocks may be less vulnerable to depletion than hunted game populations. Nonetheless, the strong negative relationship between both game and fish CPUE and distance to the urban center indicates that these resource populations may be significantly affected by the overall footprint of human activities. This should be carefully assessed in order to ensure the long-term sustainability of current extractive practices across the study area.

Our study shows that the flood pulse dynamics have direct effects on the exploitative patterns of Amazonian rural populations. We therefore expect that potential disturbances of the flood regime will have profound consequences for both hunting and fishing activities. The Amazon region is experiencing a rampant increase in the number and distribution of hydroelectric dams (Tollefson 2011; Finer & Jenkins 2012), which threatens to disrupt current patterns of natural resource extraction by rural Amazonian populations (Silvano et al. 2009). Direct impacts of dams on migratory fish, for example, are likely to provoke declines in these populations (Barthem et al. 1991; McAllister et al. 2001; Sá-Oliveira et al. 2015), thereby intensifying hunting at the time of the year when local populations rely most heavily on these migratory fish species. Climate change could also alter the flood pulse dynamics (Malhi et al. 2008), and should be carefully considered in regional conservation strategies.

More intensive law enforcement directed to harvest-sensitive fish stocks in the Amazon coincides with the reproductive and migratory season of highly pursued species.

Conversely, our results show that hunters pursued forest game species more intensively during the high-water season, suggesting that law enforcement to protect these exploited species is likely to be most effective during this period of the year.

Protein is one of the most limited nutritional resources for subsistence rural populations across the Amazon Basin (Gross 1975; Bailey et al. 1989; Headland 1991). Few alternative sources of protein and fat may be found other than aquatic and terrestrial vertebrates. Invertebrates and edible plant parts are available (Beckerman 1979; Paoletti et al. 2000), but it is unlikely that these items may provide a reliable and sufficiently ample source of protein and fat for local human populations. This underlines the key importance of game vertebrates and fish stocks for human populations, which have been limited in both numbers and distribution by animal protein since the arrival of paleo-Indians in the Amazon (Bush et al. 2015). Freshwater fisheries annually provide more than 266,000 tonnes of fish in Brazil alone (FAO 2014). Fisheries are also important sources of income for most Amazonian villages (Bennett & Thorpe 2008) and it is likely that a decrease in fish stocks will equally affect the environment, protein consumption, income, and wellbeing. Sustainable strategies for the exploitation of wild fish populations are highly desirable in such context, and successful management of oxbow lakes (Almeida et al. 2009) and specific fish species (Castello et al. 2009) are feasibility strategies in the Amazon region. Other alternatives, such as aquaculture, are still incipient in the tropics (Hall et al. 2013) and may also be a sound alternative to meet local nutritional demands and mitigate the impacts of extractive activities on local faunal populations.

5. Conclusions

Rural Amazonians hold a complex set of strategies to overcome the intermittent availability of the natural resources that they exploit. This is evident from the interconnection between fish and game extraction rates by rural Amazonian populations observed in this study. The dynamic interplay between these two extractive activities suggests that both fish and game must be considered simultaneously when planning for the sustainable harvest of natural resources right across lowland Amazonia. In a future that promises to deliver dramatic changes to the hydrological cycle of Amazonian rivers, it will be important to consider the intricate relationships between these distinct faunal communities to both safeguard the persistence of aquatic and terrestrial faunas and meet the metabolic needs of growing numbers of rural and urban Amazonians.

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Table 1. List of top-ranked candidate models ($\Sigma_{\omega} \leq .95$), and their respective Akaike's information criterion with small sample bias adjustment (AIC_c), the difference between a given model and the best model (ΔAIC_c) and the Akaike weights (ω_i). Predictors: WTD: river water discharge, WET = proportion of open wetlands within a 10-km radial buffer area, DST = Euclidean distance to the urban center, HPD: human population density within a 10 km-radius buffer area.

Stock	Response variable	Model description	AIC_c	ΔAIC_c	ω_i
Fish					
	Yield				
		WTD+WET+DST+ HPD	5649.7	0	0.434
		WTD +WET+DST	5650.2	0.55	0.329
		WTD +WET+ HPD	5651.4	1.75	0.181
	CPUE				
		WTD +WET+DST	3992.7	0	0.531
		WTD +WET+DST+ HPD	3994.8	2.04	0.191
		WTD +DST	3996.6	3.85	0.077
		WTD +WET+ HPD	3997	4.3	0.062
		WTD +WET	3997.1	4.32	0.061
Game					
	Yield				
		WTD	11517.8	0	0.391
		WTD + HPD	11519.1	1.3	0.204
		WTD +DST	11519.6	1.83	0.156
		WTD +WET+ HPD	11521.1	3.31	0.075
		WTD +WET	11521.6	3.78	0.059
		WTD +WET+DST	11521.6	3.84	0.057
	CPUE				
		WTD +DST	2130	0	0.298
		DST	2131.5	1.51	0.141
		WTD +WET+DST	2132	2.02	0.109
		WTD +DST+ HPD	2132	2.05	0.107
		WET+DST	2132.2	2.29	0.095
		WTD +WET+DST+ HPD	2132.6	2.63	0.08
		DST+ HPD	2133.5	3.55	0.051
		WET+DST+ HPD	2134.3	4.33	0.034
		WTD	2135	5.07	0.024

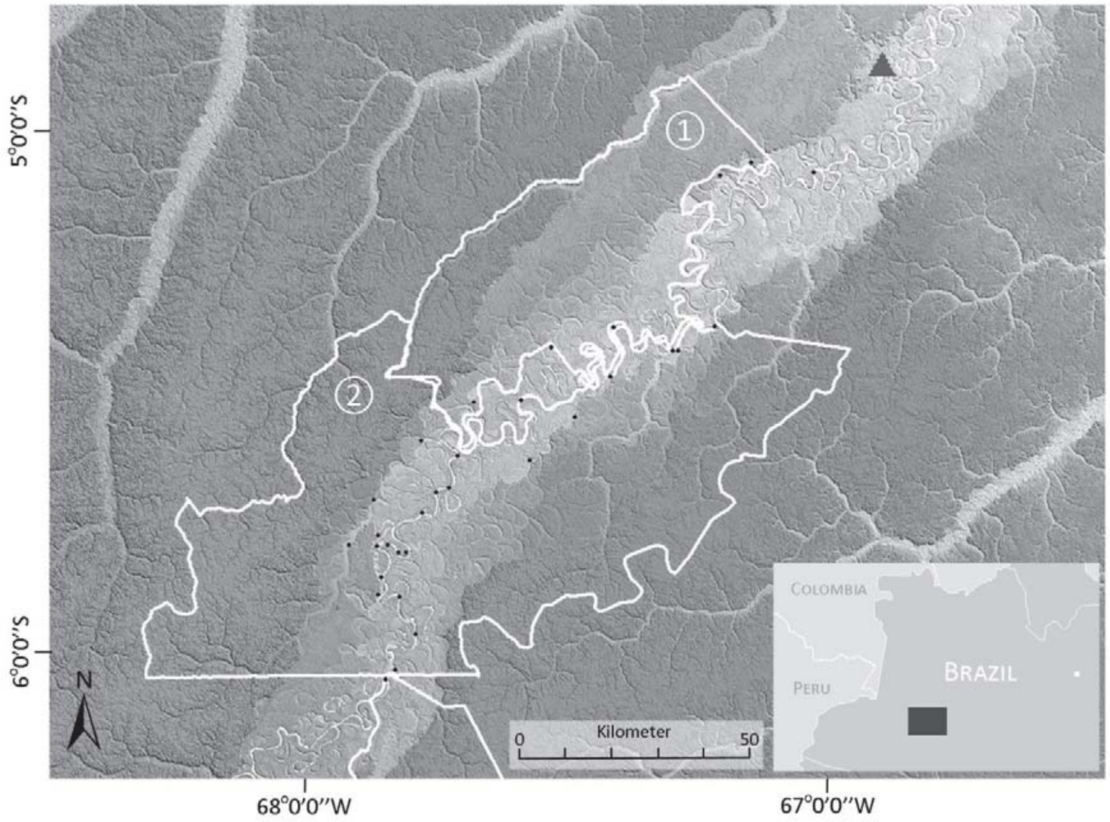

Figure 1. Map of the study area showing the two contiguous conservation units, (1) Médio-Juruá Extractive Reserve, (2) Uacarí Sustainable Development Reserve, all surveyed villages (black dots), and the urban center of the municipal county of Carauari (solid triangle). Várzea and terra firme forests are shown by light and dark grey areas, respectively.

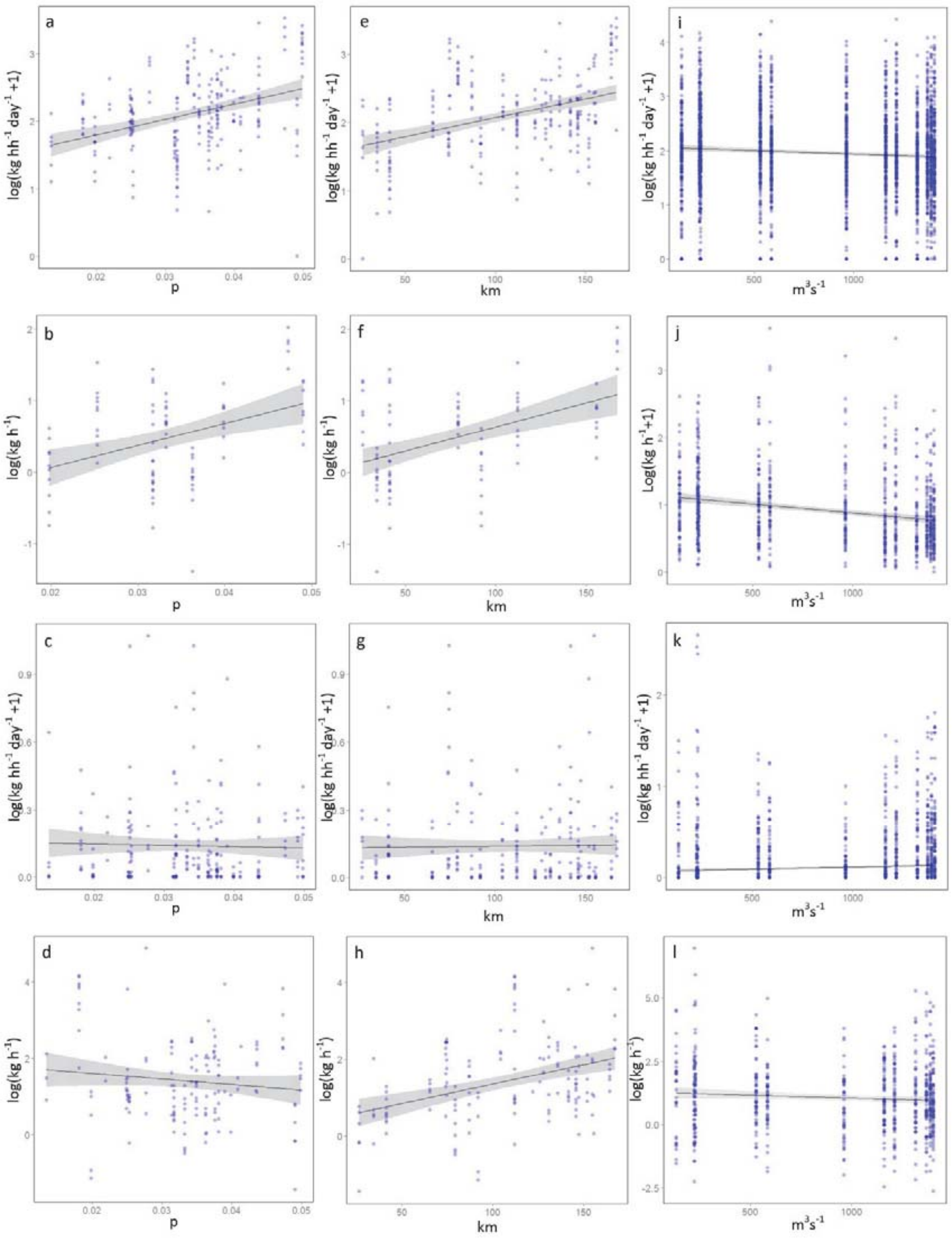

Figure 2. Relationships between (a) mean annual fish yield and proportion of open wetlands, (b) mean annual fish CPUE and proportion of open wetlands, (c) mean annual game yield and proportion of open wetlands, (d) mean annual game CPUE and proportion of open wetlands, (e) mean annual fish yield and distance to the urban center, (f) mean

annual fish CPUE and distance to the urban center, (g) mean annual game yield and distance to the urban center, (h) mean annual game CPUE and distance to the urban center, (i) mean annual fish yield and river water discharge, (j) mean annual fish CPUE and river water discharge, (k) mean annual game yield and river water discharge, and (l) mean annual game CPUE and river water discharge. The 95% confidence intervals are shown in grey.

Table S1. Summary of generalized linear mixed model (GLMM) results, with top-ranked models listed. LL = log-likelihood; AICc = Akaike's information criterion for small sample sizes; ΔAICc = difference between a lower ranked models and the best model in units of AICc; ω_i = Akaike weight; * = included variables, β = standardized coefficients; SE = standard error; AW: model averaged Akaike weights for each parameter. Predictors: WTD: river water discharge, WET = proportion of open wetlands within a 10-km radius buffer area, DST = Euclidean distance to the urban center, HPD= human population density within a 10-km radius buffer area, GMY=game yield. Predictors presenting a strong relationship with response variable (β ± SE does not overlap 0) are written in bold type.

Table S1.a. Multimodel Inference: Fish Yield ($\log_{10}$+1).

Model rank	intercept	WTD	WET	DST	HPD	LL	AICc	ΔAICc	ω_i
1	1.727	**-0.000129**	**23.90**	**0.003748**	**-0.001135**	-2814.791	5649.7	0.00	0.434
2	1.361	**-0.000129**	**21.57**	**0.005344**	**-**	-2816.075	5650.2	0.55	0.329
3	2.238	**-0.000128**	**26.31**	-	**-0.001867**	-2816.674	5651.4	1.75	0.181
β	1.698	**-0.000128**	**23.57**	**0.004423**	**-0.001344**				
SE	0.46	**0.000034**	**7.695**	**0.001956**	**0.000757**				
AW .95	**1.00**	**1.00**	**1.00**	**0.81**	**0.65**				

Table S1.b. Multimodel Inference: Fish CPUE ($\log_{10}$).

Model rank	intercept	WTD	WET	DST	HPD	LL	AICc	ΔAICc	ω_i
1	-1.197	**-0.000798**	**79.94**	**0.01581**	-	-1987.262	3992.7	0.00	0.531
2	-1.262	**-0.000798**	**79.74**	**0.01616**	0.000176	-1987.259	3994.8	2.04	0.191
3	1.528	**-0.000795**	**-**	**0.01676**	-	-1990.210	3996.6	3.85	0.077
4	0.7417	**-0.000793**	**86.77**	**-**	-0.003424	-1989.413	3997.0	4.30	0.062
5	-0.01242	**-0.000794**	**85.76**	**-**	-	-1990.445	3997.1	4.32	0.061
Β	-0.773219	**-0.000797**	**80.81**	**0.01598**	-0.00070				
SD	1.474244	**0.0002**	**29.09**	**0.00581**	0.00273				
AW .95	**1**	**1**	**0.92**	**0.87**	0.27				

Table S1.c. Multimodel Inference: Game Yield ($\log_{10}$+1).

Model rank	intercept	WTD	WET	DST	HPD	LL	AICc	ΔAICc	ω_i
1	1.0320	**0.005738**	-	-	-	-5751.881	11517.8	0.00	0.391
2	1.2490	**0.0005742**	-	-	-0.0009294	-5751.523	11519.1	1.30	0.204
3	0.8895	**0.0005733**	-	0.0012970	-	-5751.789	11519.6	1.83	0.156
4	1.2140	**0.0005743**	1.1120	-	-0.0009397	-5751.519	11521.1	3.31	0.075
5	0.9979	**0.0005704**	1.2170	-	-	-5752.764	11521.6	3.78	0.059
6	0.9090	**0.0005732**	-0.6072	0.0013060	-	-5751.788	11521.6	3.84	0.057
β	1.0601	**0.000574**	0.63	0.0013	-0.000934				
SE	0.346	**0.000109**	13.652	0.0030	0.0011				

AW .95		**1**	0.20	0.23	0.30

Table S1.d. Multimodel Inference: Game CPUE ($\log_{10}$).

Model rank	intercept	WTD	WET	DST	HPD	LL	AICc	ΔAICc	ω_i
1	0.3127	**-0.000225**	**-**	**0.00831**	-	-1056.867	2130.0	0.00	0.298
2	0.06607	-	**-**	**0.00849**	-	-1058.645	2131.5	1.51	0.141
3	0.8141	**-0.000218**	**-15.96**	**0.00857**	-	-1056.848	2132.0	2.02	0.109
4	0.3395	**-0.000225**	**-**	**0.00822**	-7.128e-5	-1056.865	2132.0	2.05	0.107
5	0.5325	**-**	**-14.42**	**0.00867**	-	-1058.010	2132.2	2.29	0.095
6	0.7699	**-0.000232**	**-15.87**	**0.00873**	1.697e-4	-1056.125	2132.6	2.63	0.080
7	0.09646	**-**	**-**	**0.00839**	-8.070e-5	-1058.642	2133.5	3.55	0.051
8	0.4871	**-**	**-14.67**	**0.00886**	1.418e-4	-1058.003	2134.3	4.33	0.034
9	1.254	**-0.000237**	**-**	**-**	-	-1060.428	2135.0	5.07	0.024
β	0.4166	**-0.0002254**	**-15.34**	**0.008459**	0.000025				
SE	0.5571	**0.0001183**	**0.00123**	**0.002975**	0.001226				
AW .95		**0.66**	**0.34**	**0.97**	0.29				

Table S1.e. Multimodel Inference: Fish yield ($\log_{10}$+1), including game yield as a fixed parameter in the global model.

Model rank	intercept	GMY	WTD	WET	DST	HPD	LL	AICc	ΔAICc	ω_i
1	0.39320	**-0.06195**	**-0.000039**	**21.65**	**0.003873**	**-0.0007802**	-42050.53	84117.1	0.00	0.596
2	0.39050	**-**	**-0.00004**	**21.68**	**0.003882**	**-0.0007798**	-42052.61	84119.2	2.16	0.203
3	0.35890	**-0.06393**	**-**	**21.81**	**0.003842**	**-0.0007955**	-42053.14	84120.3	3.23	0.119
4	0.35530	**-**	**-**	**21.85**	**0.003851**	**-0.007955**	-42055.36	84122.7	5.65	0.035
β	0.3882	**-0.06228**	**-0.000039**	**21.61**	**0.00393**	**-0.0007826**				
SE	0.1490	**0.03039**	**0.000017**	**2.989**	**0.00076**	**0.0002739**				
AW .95		**0.78**	**0.87**	**1.00**	**1.00**	**1.00**				

Figure S1. Images from the Médio-Juruá Extractive Reserve depicting the seasonal changes in the landscape due to a strong seasonal variation in river water level. Photos taken (A) during the high-water season (04 May 2009) at the Morada Nova community, and (B) during the low-water season (10 July 2010) at exactly the same place.

PAPER II

Paper II evaluates the influences of hunting practiced by native Amazonians (i.e. Matsigenka indigenous groups) on game community structure and composition by comparing hunted and unhunted sites within Manú National Park, Peru.

Photo: W. Endo

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Game Vertebrate Densities in Hunted and Nonhunted Forest Sites in Manu National Park, Peru

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ABSTRACT

Manu National Park of southern Peru is one of the most renowned protected areas in the world, yet large-bodied vertebrate surveys conducted to date have been restricted to Cocha Cashu Biological Station, a research station covering < 0.06 percent of the 1.7 Mha park. Manu Park is occupied by > 460 settled Matsigenka Amerindians, 300–400 isolated Matsigenka, and several, little-known groups of isolated hunter–gatherers, yet the impact of these native Amazonians on game vertebrate populations within the park remains poorly understood. On the basis of 1495 km of standardized line-transect censuses, we present density and biomass estimates for 23 mammal, bird, and reptile species for seven lowland and upland forest sites in Manu Park, including Cocha Cashu. We compare these estimates between hunted and nonhunted sites within Manu Park, and with other Neotropical forest sites. Manu Park safeguards some of the most species-rich and highest biomass assemblages of arboreal and terrestrial mammals ever recorded in Neotropical forests, most likely because of its direct Andean influence and high levels of soil fertility. Relative to Barro Colorado Island, seed predators and arboreal folivores in Manu are rare, and generalist frugivores specializing on mature fruit pulp are abundant. The impact of such a qualitative shift in the vertebrate community on the dynamics of plant regeneration, and therefore, on our understanding of tropical plant ecology, must be profound. Despite a number of external threats, Manu Park continues to serve as a baseline against which other Neotropical forests can be gauged.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: bushmeat; defaunation; distance sampling; forest vertebrates; hunting; indigenous people; Manu National Park; trophic cascade.

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THE LONG-TERM OCCUPATION OF TROPICAL FOREST reserves by indigenous peoples has fuelled a vigorous debate between those who view indigenous peoples as conservation allies and those who see them as a threat to the long-term viability of wildlife populations (Harmon 1987, Redford 1991, Alcorn 1993, Redford & Stearman 1993, Robinson 1993, Peres 1994, Zimmerman *et al.* 2001, Shepard 2002, Terborgh & Peres 2002, da Silva *et al.* 2005, Nepstad *et al.* 2006, Ohl-Schacherer *et al.* 2007, Shepard *et al.* in press). A well-known skirmish appeared in the pages of *Conservation Biology*, triggered by Terborgh's (1999) warning that the Westernizing and fast-growing Matsigenka indigenous population within Peru's Manu National Park, located in the southeastern Peruvian Amazon, will eventually degrade Manu's biological integrity unless some way is found to promote voluntary resettlement outside the park (Redford & Sanderson 2000, Schwartzman *et al.* 2000, Terborgh 2000, Peres & Zimmerman 2001).

Since its creation in 1973, Manu Park has been considered one of the world's most important tropical protected areas. It constitutes the core area of a UNESCO Biosphere Reserve, is located in one of the most species-rich biodiversity hotspots, and is a World Heritage Site. Manu Park is remarkable not only for its high level of biological diversity, including a wide array of different habitats with distinct faunal and floral compositions, but also for the apparently high abundance of many species that are threatened or rare elsewhere, probably because of its soil nutrient-rich eutrophic forests, arguably some of the most fertile in the Neotropics (Foster 1990, Ohl *et al.* 2007). The 1.7 Mha Manu Park covers the watershed of the Manu River, including large stretches of lowland tropical rainforest. Over most of the park, the vegetation is characterized by a mosaic of different types of tropical lowland rainforest on both recently formed, inundated alluvial floodplains (lowland forest) and older, elevated, and hilly terraces (upland or terra firme forest) (see Terborgh 1990, Terborgh *et al.* 1996, Shepard *et al.* 2001), although the southwestern portion of the park includes an Andean elevational gradient (*ca* 340–3450 m asl), ranging from montane rain forest through cloud forest, the mossy, low canopy *elfin forest*, and Andean grassland (*puna*).

The core of Manu Park is officially considered as an 'untouchable area', where only nonintrusive activities such as research are permitted. But when the park was established in 1973, Peruvian law did not yet recognize the indigenous populations that were known to be present. In the years following park establishment, however, several laws granted ancestral populations the right to remain within protected areas, provided that their traditional subsistence activities did not interfere with the park's conservation goals. Thus, in a legal contradiction, the Manu Park core area is inhabited by a considerable indigenous population. As of late 2007, there

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were > 460 Matsigenka people settled mostly in two state-recognized communities inside Manu Park's core area, growing at an annual rate of *ca* 4 percent or more (Fig. 1). The Tayakome settlement was founded by missionaries in the early 1960s, and the Yomybato settlement dates from the late 1970s. Three to four hundred more isolated Matsigenka reside in remote settlements in the Manu headwaters, and there are unknown numbers of uncontacted hunter–gatherers, in total almost certainly surpassing 1000 people (see also Shepard *et al.* in press). The Matsigenka populations engage in swidden agriculture, growing manioc, bananas, maize, and diverse minor crops (Ohl *et al.* 2007). They fish with traditional and modern technology, but due to park gun restrictions and the high cost, they hunt mainly with bow-and-arrow (Ohl-Schacherer *et al.* 2007). Three to four hundred more isolated Matsigenka reside in remote settlements in the Manu headwaters, mostly > 600 m asl. There are at least two small groups of elusive, nomadic foragers in Manu Park of unknown population size: a Mashco-Piro population in the headwaters of the Pinquen River that has been sighted occasionally on the southern bank of the lower Manu for decades (Kaplan & Hill 1984), and another group, possibly also Mashco-Piro, that has migrated more recently towards the north bank tributaries of the middle and upper Manu, apparently fleeing petrochemical companies and loggers who moved into the adjacent Rio de las Piedras in the mid-1990s (Shepard *et al.* in press). Both of these groups have actively avoided and rejected all contact, both with outsiders and with local indigenous groups, perhaps fearful of the toll of introduced diseases.

At present, the main biodiversity threat posed by humans is the reduction in large-bodied vertebrate game populations caused by overhunting (Terborgh 1999, Shepard *et al.* in press). Yet Manu Park retains a full complement of large mammal (Terborgh 1983, Janson & Emmons 1990) and gamebird species (Terborgh *et al.* 1990) and most of the Park area has been subjected to light or no hunting pressure (Ohl-Schacherer *et al.* 2007).

Efforts to resolve people–park conflicts in Manu begin with reliable estimates of terrestrial vertebrate abundances, especially game species. However, most research on vertebrate populations in Manu Park has been concentrated at a single lowland forest site, Cocha Cashu Biological Station (11.88826° S, 71.40756° W), which is situated at the edge of an oxbow lake in an alluvial plain inside a mature lowland forest. It is unclear to what extent faunal density estimates obtained within the 10 km^2 study area of Cocha Cashu Biological Station (accounting for < 0.06% of the park area) can be extrapolated to the entire park or even just to areas <600 m, which are primarily comprised of upland forest. Tropical forest vertebrate surveys across the Amazon basin and elsewhere reveal great spatial variability in population abundance and community composition. Some of this variability can be explained by baseline environmental variables, such as geomorphology and soil fertility (Barnes & Lahm 1997; Peres 2000, 2008), some by biogeography (Ayres & Clutton-Brock 1991, Primack & Corlett 2005), and an increasing amount by anthropogenic disturbance, including hunting (Peres & Palacios 2007).

In this study, we used standardized line-transect surveys to characterize the mid- and large-bodied terrestrial vertebrate assemblage (including all major game species) at seven forest sites within Manu Park. Two sites are heavily hunted by Matsigenka native communities, and five have not been subjected to hunting for at least 35 yr. Surprisingly, given the long research history of Cocha Cashu (Gentry 1990), the large vertebrate assemblage at this site has never been censused systematically using this technique, although diurnal primates were censused along the main trail system by Janson and Terborgh (1980) in July 1974. This study therefore presents the first estimates of large vertebrate abundances in Manu Park that allow us to (1) compare the two major forest types < 600 m asl; (2) compare against previous abundance estimates at Cocha Cashu, which were based on a variety of census techniques; (3) compare against forest sites elsewhere in the Neotropics; and

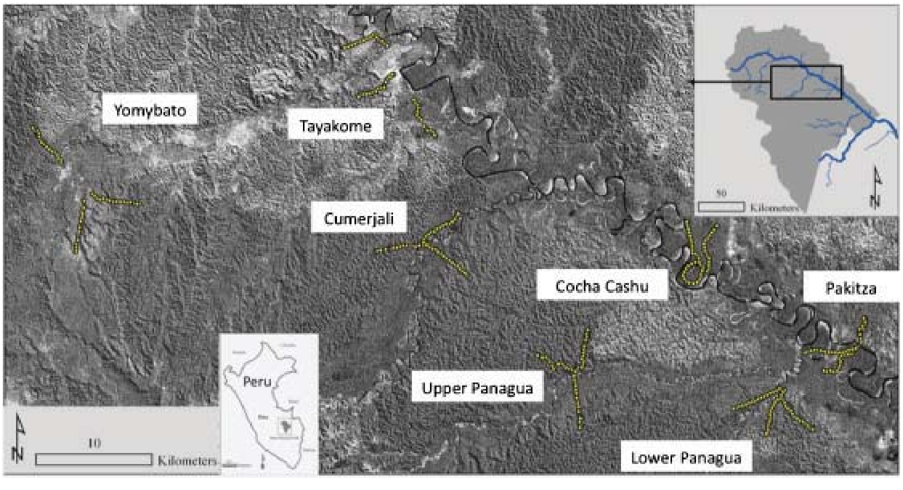

FIGURE 1. Map of the seven census sites in Manu National Park. Dotted lines are the individual line transects. The Tayakome and Yomybato sites are the two Matsigenka villages. At the villages, the censuses started at the perimeter of the inhabited areas, accounting for the space between the trailheads. Light-color forests (upper left and upper-right corners) are dominated by either bamboo (*Guadua* spp.) or *Cecropia sciadophylla*. Upper inset, map of Manu Park; Lower inset, Peru, showing the location of Manu Park.

finally (4) quantify the effects of Matsigenka subsistence hunting on vertebrate species composition and population abundance.

METHODS

STUDY SITES.—The study was conducted at seven locations inside Manu Park, at altitudes of 340–420 m asl (Table S1; Fig. 1). Pairwise distances between the census sites (measured from the central campsites) ranged from 8 to 70 km (mean ± SD distance between sites = 32 ± 17 km). Annual rainfall averages 2000–2600 mm, with a dry season between May and September/October. Away from the high-elevation, Andean portion of the park, the mean temperature is fairly constant, but in the dry season, there can be several-day cold fronts (*friajes*) that reach as low as 9°C, thereby reducing animal activity.

The two major Matsigenka settlements, Tayakome and Yomybato, are located on upland terraces, 10–50 m above the Manu River (Fig. 1; Shepard *et al.* 2001). About 200 people live in each of these two permanent communities. The rest of the population is found in smaller, less stable satellite settlements. The five nonhunted census sites are 15–70 km from any Matsigenka settlement. The Cumerjali tributary is occasionally visited by hunters on long-distance forays, but the Upper and Lower Panagua sites have not been visited by Matsigenka hunters within at least the last two generations (although we cannot completely rule out transient forays by uncontacted indigenous people), and both Cocha Cashu Biological Station and the Pakitza guard post have been protected from hunting since at least the Park's founding in 1973.

The Cocha Cashu and Pakitza census sites were exceptions in two ways. Firstly, these were the only two sites located exclusively in lowland forest. Secondly, at Cocha Cashu, one transect circled the oxbow lake rather than radiating outward. At Pakitza, the third, northern transect (Fig. 1) was abandoned after the presence of an uncontacted indigenous group was detected, which also prevented us from conducting censuses upriver of Tayakome or near the mouth of the Manu River.

All census transects were 1 m wide, marked every 50 m, georeferenced with a Garmin GPS60 (Garmin International Inc., Olathe, KS, U.S.A.) with external antenna, and mapped in relation to forest topography (Fig. 1). In most sites, we censused three, nonspatially independent transects radiating outwards from the central campsite or Matsigenka settlement. The transects in the two Matsigenka settlements were deliberately placed within the zones of high Matsigenka hunting effort (Fig. 1; see Ohl-Schacherer *et al.* 2007 for further site descriptions).

Excluding one transect at Tayakome and three at Cocha Cashu, all trails were opened specifically for this study, minimizing possible bias caused by previous human interference in the area. In total, 20 transects, totaling 90 km, were censused. All cut transects were left to rest for at least a day before being censused.

There is no way that we can correct statistically or otherwise for the local hunting pressure exerted by nomadic indigenous foragers such as the Mashco Piro. For ethical and safety reasons, we cancelled census efforts, where their presence was evident, also effectively minimizing any transitory impacts of their hunting activities on our census data. The extremely high abundance of vertebrate game species recorded in our 'nonhunted' sites, in contrast to the noted reductions in abundance around sedentary indigenous settlements, further attests to the ephemeral and minimal impact of hunting by nomadic peoples.

LINE-TRANSECT SURVEYS.—Our line-transect censuses focused on medium to large-bodied diurnal vertebrates because these species can be detected visually and/or acoustically, are the preferred game species among indigenous hunters (Ohl-Schacherer *et al.* 2007), and represent a disproportionate fraction of the total vertebrate biomass in tropical forests (Terborgh 1983, Peres 1999a). For each animal sighting, we recorded the time, species, perpendicular distance from the transect (PD), group size, detection mode (*e.g.*, visual or acoustic), group diameter for large, uncohesive groups or subgroups (as often occurs in large group-living primates), and distance along the transect. Detection rates naturally decline with PD, but given a sufficient number of independent observations, the PD distribution can be modeled to calculate an 'effective strip width' using the program Distance v. 4.1 (Buckland *et al.* 1993), which is then used to generate a group or population density estimate based on the number of group or single-animal encounters.

Censuses were conducted from January to July 2006, thus, in the late rainy and early dry season. No census was conducted in May, the month with the highest frequency of *friajes*, when animal activity can be atypically low. Trails were walked on rainless days during the morning (0630–1030 h) and afternoon (1300–1700 h) by two observers (a wildlife biologist and a local Matsigenka hunter) at a mean velocity of 1.2 km/h. All trailheads were placed > 400 m from campsites or from any Matsigenka houses. Each transect in five of our seven sites were surveyed for *ca* 10 d, usually within a 21-day period (for a detailed description of our census procedures, see Peres 1999b). However, Cocha Cashu, and Pakitza were censused over multiple days interspersed between February and July (Table S1), making comparisons with historical abundance estimates at these sites more reliable. Seasonal changes may affect the detectability or even the spatial distribution of some species (Haugaasen & Peres 2007), so to partially control for this effect with respect to the nonhunted vs. hunted comparison, one Matsigenka settlement was censused in the rainy season (Yomybato), and one in the dry season (Tayakome; Table S1).

TAXONOMIC TREATMENT.—Mammal species nomenclature follows Solari *et al.* (2006), with some adjustments made by the authors. Unfortunately, due to the rapidly changing nature of mammalian alpha-taxonomy, in some places the Latin and common names differ from those used in previous publications from the area (including Janson & Emmons 1990, Ohl-Schacherer *et al.* 2007). To facilitate comparison with previous publications, we provide both current and older Latin names in Tables 1 and S2 or in the text. Bird nomenclature follows Walker *et al.* (2006) and is consistent with Ohl-Schacherer *et al.* (2007).

SPECIES ABUNDANCE ESTIMATES ANALYSIS.—For each species surveyed, we calculated the encounter rate (per 10 km walked, ER). We also

TABLE 1. *Abridged table of population density estimates at the different sites censused in Manu National Park.* D$_{ind}$, *density of individuals (/km^2); U, upland, terra firme forest; L, lowland, floodplain forest. Densities not calculated for species with low sample sizes (see text). Tayakome and Yomybato are the two hunted sites. White-lipped peccary population density estimates derived on the basis of a global model stratified by site-specific encounter rates, in which sampling units are defined as small clusters of peccaries (*N = *93) sighted from the transect. See Table S2 for a complete version, including explanations for footnotes.*

	Yomybato, hunted, U	Tayakome, hunted, U	Upper Panagua, U	Lower Panagua, U	Pakitza, L	Cumerjali, U	Cocha Cashu, L
Taxa	D_{ind}	D_{ind}	D_{ind}	D_{ind}	D_{ind}	D_{ind}	D_{ind}
Primates							
Saimiri boliviensis	–	4	10.8	29.3	47.9	15.8	49.7
Saguinus fuscicollis	37	5.3	37.8	53.3	29.9	43	12.7
Saguinus imperator	–	1.6	–	–	–		6
Callicebus bruneus[3]	7.8	5.2	18.6	20.2	4.3	12.3	5.8
Pithecia irrorata[5]	4.8	1.9	–	–	–	2.3	1.1
Cebus apella	11.2	6	15.5	30.1	30.2	17.1	28.2
Cebus albifrons	1.8	2.5	11.9	10.1	22.8	7.4	22.5
Alouatta sara[1]	0.7	8.3	12.2	11.4	6.3	17	8.6
Lagothrix cana[4]	7.6	9.7	13.2	39.1	48.5	34.1	1.2
Ateles chamek[2]	2.3	7.8	45.9	41.7	14	49	36.3
Ungulates							
Mazama spp.[6]	1	2.7	3.21	1.45	1.68	4.68	2.49
Pecari tajacu[7]	7.8	3.78	8.2	5.17	2.25	5.8	8.03
Tayassu pecari	1.1	5.8	9.2	21.7	43.8	32.4	15
Rodentia							
Dasyprocta variegata	–	1.64	0.99	1.88	1.826	1.722	3.47
Myoprocta pratti	0.5	0.53	2.2	0.53	0.55	1.65	1.14
Sciurus spp.[8]	2.49	15	39.7	16.4	11.61	14.77	9.72
Birds							
Crypturellus spp.[10]	17.72	12.8	16.1	15.9	29.51	15.28	16.03
Tinamus spp.[11]	5.52	8.27	6.46	7.32	12.36	26.92	11.59
Mitu tuberosum	0.62	2.12	5.9	8.9	12.18	7.89	2.73
Odontophorus gujanensis	89.3	69.1	50.2	48.6	13.64	86.8	15.47
Penelope jacquacu	34.74	12.6	20.2	13.7	2.24	29.34	4.58
Pipile cumanensis	–	1.55	0.53	1.55	0.25	1.07	0.74
Psophia leucoptera	5.42	13.7	52.7	37.4	14.95	20.39	23.89

calculated group (D_{grp}) and population (individual) densities (D_{ind}) when a sufficient number of independent detection events was available across all the sites, or, in the case of the emperor tamarin (*Saguinus imperator*), when we could apply the detection functions derived from the more abundant saddle-back tamarin, (*S. fuscicollis*). Only encounter rates are presented for rare species (*e.g.*, felids, coatis, tayras), here defined as those detected fewer than 39 times, with a few exceptions: brown agouti (*Dasyprocta variegate*; $N_{\mathrm{sightings}} = 38$), brocket deer (*Mazama* spp., 37), green acouchy (*Myoprocta pratti*, 13), blue-throated piping guan (*Pipile cumanensis*, 16), and gray-monk saki (*Pithecia irrorata*, 16), for which available data still allowed us to construct more error-prone but reasonable detection curves. On a site-by-site basis, data obtained during afternoon census walks were included in the analysis only when density estimates for any given species including both the morning and afternoon data did not differ by > 20 percent from estimates based on morning census data only. This is because while several diurnal species exhibit an activity peak during early- to mid-morning hours, others exhibit a more markedly bimodal distribution of activity (Hill *et al.* 1997, Peres 1999b).

Analysis of Variance (ANOVA) tests revealed that species-specific PD distributions were not significantly different across sites, once a handful of outlier observations were removed from the dataset (typically, acoustic records of vocally conspicuous primate groups > 50 m from the transect). This allowed us to pool the PD values across census sites and thereby obtain a single, more robust probability distribution of encounter distances for each species. Following Buckland *et al.* (1993), density estimates were derived by always choosing the best-fit models as judged by the lowest number of parameters and coefficients of variation, series expansions, and AIC values. Extreme PD values were also truncated whenever necessary to improve model convergence and avoid including outliers that could bias model estimators, especially vocally conspicuous group living species. Further details are given in Appendix S1.

For each species, mean (sub)group sizes were calculated using the mean values of all (sub)group counts obtained from transects within a site, thus considering each site as an independent group of values. For primate species foraging in large, uncohesive groups for which whole-group counts tend to be incomplete, we recorded multiple observations, sizes, and PDs of each subgroup (cluster) encountered along the same transect walks, even if they were < 500 m apart and likely belonged to the same social group (or 'community' in the case of spider monkeys). This sampling approach reduces the variance in cluster size, need not assume complete spatial independence between neighboring clusters or feeding parties, and has the advantage of boosting sample sizes and overall model fitness (S. Buckland, pers. comm.). For some large group-living primate species (*e.g.*, gray woolly monkeys *Lagothrix cana* and Peruvian spider monkeys *Ateles chamek*), which can move in fairly uncohesive groups, we also considered the cluster spread in the analysis, thereby minimizing density overestimates (Peres 1997a). Thus, the cluster density, D_{clt}, is

$$D_{\mathrm{clt}} = \frac{N}{2L\left(ESW + \frac{CSp}{3}\right)}$$

where N = number of cluster detections, L = km walked, ESW = effective strip width, and CSp = cluster spread, *i.e.*, mean diameter of the cluster. Individual population density D_{ind} is calculated by multiplying D_{clt} against the mean cluster size for that site.

BIOMASS ESTIMATES.—Population biomass densities were calculated by multiplying the individual population density (D_{ind}), if available, against 80 percent of each species' mean adult body mass estimated from whole carcasses weighed in the Matsigenka communities, using a hunter offtake dataset consisting of 2089 kills and 102,397 consumer-days sampled between October 2004 and September 2005 (Ohl-Schacherer *et al.* 2007). However, for those primate species that are markedly sex dimorphic, we calculated the mean body mass as the mean of adult female and adult male weights, using a dataset from Peres (1999a). Also, for both genera of tinamous (*Tinamus* and *Crypturellus*), the mean body mass was calculated at the level of genus from a Cocha Cashu dataset (Terborgh *et al.* 1990).

For white-lipped peccaries (*Tayassu pecari*), which can form large, uncohesive herds of well over 600 individuals that often move rapidly across the landscape, we were unable to derive a reliable population density estimate (D_{ind}; Tables 1 and S2). However, we conservatively estimate the density and biomass of clusters detected from all transects, which were then multiplied against the mean cluster size (D_{clt}; Tables 1 and S2) based on reliable subgroup counts. Subgroups are merely defined as a cluster of individuals observed simultaneously within 50 m of the transect (range = 1–23). These clusters of animals were, however, but a small part of much larger herds which could be heard up to 400 m from the transects. In total, we detected 93 clusters of white-lipped peccaries belonging to at least 22 different herds at the seven sites. Population biomass was then calculated by multiplying density estimates by 80 percent of the mean body weight of animals harvested by Matsigenka hunters (Ohl-Schacherer *et al.* 2007). Silman *et al.* (2003) report that minimum group counts numbered between 90 and 138 in 1978, just before they disappeared, and after their reappearance in 1990 and subsequent population recovery, and herd sizes considerably larger than 100 individuals have been regularly observed near Cocha Cashu Biological Station.

COMMUNITY ANALYSIS.—Constrained correspondence analysis (CCA) was performed on the community-wide population density dataset (Tables 1 and S2) using the function cca from the package vegan 1.13-2 (Oksanen *et al.* 2007) in the statistical program R 2.7.2 (R Development Core Team 2007). We used 21 species, omitting the patchily distributed and rare primate species *Saguinus imperator* and *Pithecia irrorata*, but otherwise using all species for which sightings were sufficient to be able to estimate a population density D_{ind} in at least one site, setting $D_{\mathrm{ind}} = 0$ in the rest of the sites for that species (Tables 1 and S2). The evidence for an effect of each of two categorical factors Hunting (Hunted vs. Nonhunted) and Forest type (Lowland vs. Upland) was assessed by a mock ANOVA permutation test on each factor, separately (Oksanen *et al.* 2007). We were unable to test a model with both factors because of strong collinearity (both hunted sites are in upland forest). Note, however, that the statistical power in these tests is weak, because of low sample size. The pairwise, quantitative Jaccard distance metric, $J = \frac{2B}{1+B}$, where B (Bray–Curtis dissimilarity) is $\frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})}$, where $x = D_{\mathrm{ind}}$, was used over $i = 23$ species and communities j and k. We repeated the above analyses with a biomass dataset, using the same 21 species.

RESULTS

DENSITY ESTIMATES.—Overall, 1495 km of census walks were conducted over the seven forest sites (mean ± SD = 213.6 ± 33.9 km/site), resulting in observations of 37 mammal, 17 large bodied bird, and one reptile species, all of which were partly or entirely diurnal. Of these 55 species, 23 (including white-lipped peccaries) had a sufficient number of observations to allow estimation of population density estimates, D_{ind} (Tables 1 and S2). Primates were by far the most abundant species encountered, totaling 1575 groups or 59.9 percent of all single animal or group encounters.

Although we were unable to obtain complete counts of white-lipped peccary herds, we can confirm that this species has rebounded from an almost complete regional absence that lasted from approximately 1978 to 1990 (Silman *et al.* 2003, Ohl-Schacherer *et al.* 2007), and our censuses suggest population densities of 3.4 ± 2.3 SE ind/km^2 in hunted sites and 24.4 ± 6.2 ind/km^2 in nonhunted sites (Tables 1 and S2).

The following diurnal, nocturnal, or cathemeral species were detected in low numbers, at very few sites, and primarily by indirect signs (*e.g.*, tracks, scats, active dens, fresh scratches) or vocalizations: giant armadillo (*Priodontes maximus*), South American tapir (*Tapirus terrestris*), paca (*Agouti paca*), black-headed night monkey (*Aotus nigriceps*), pygmy marmoset (*Cebuella pygmaea*), ocelot (*Leopardus pardalis*), jaguar (*Panthera onca*), puma/cougar (*Puma concolor*), kinkajou (*Potos flavus*), Allen's olingo (*Bassaricyon alleni*), and rufousvented ground cuckoo (*Neomorphus geoffroyi*). Both forest canids (bush dog *Speothos venaticus* and short-eared dog *Atelocynus microtis*), which are very rare, were visually detected. Despite the low number of direct sightings, we recorded unambiguous evidence of jaguars and/or pumas (vocalizations, tracks or scratches) at all sites, including the two hunting catchments close to Matsigenka settlements.

In addition, some typically (semi)aquatic species that were not expected to be detected from the forest transects, were observed during surveys: giant otter (*Pteronura brasiliensis*), muscovy duck (*Cairina moschata*), and horned screamer (*Anhima cornuta*). The remaining diurnal species of midsized to large vertebrates known to occur in the lowland areas of Manu Park, such as the smaller cats *Felis wiedii* and *Puma yagouaroundi*, the mustelids *Galictis vittata* and *Mustela africana*, the small primate *Callimico goeldii* and a few other animals (see Solari *et al.* 2006), were not detected due to their secretive behavior, patchy distributions, and/or low local densities.

Species abundances were generally higher in nonhunted areas than in the two hunted sites, Yomybato and Tayakome (Tables 1, 2 and S2). However, several species did not show clear decreases in abundance or were more abundant in one or both hunted sites: brocket deer (*Mazama* spp., mainly *M. americana*), saddle-back tamarin (*Saguinus fuscicollis*), gray monk saki (*Pithecia irrorata*), collared peccary (*Pecari tajacu*), Spix's guan (*Penelope jacquacu*), marbled wood quail (*Odontophorus gujanensis*), and small tinamous (*Crypturellus* spp.). Finally, we report a minor range extension. Emperor tamarins (*Saguinus imperator*), which were previously known only from sites on the north (left) bank of the Manu River, also occur on the south (right) bank of the Manu River, at Tayakome.

BIOMASS ESTIMATES.—We first examine the five nonhunted sites and derive a conservative total biomass estimate for each site by excluding white-lipped peccaries, for which our abundance estimates are less reliable (Table 2). In the five sites, primates account for a mean of 69 percent (range = 61–79%) of this conservative total, showing their disproportionate biomass contribution to the overall diurnal vertebrate community. Large-bodied ateline primates alone (*i.e.*, woolly monkeys and spider monkeys) were particularly strongly represented in several nonhunted sites, accounting for a mean of 48 percent (range = 36–55%) of the total biomass estimate across all sites. The highest total primate biomass estimates recorded were in the nonhunted Lower Panagua and Cumerjali sites, with a total of 779.9 and 774.9 kg/km^2, respectively.

Unexpectedly, and despite enjoying a reputation as having one of the highest recorded biomass densities in Neotropical forests (Janson & Emmons 1990), our conservative estimate of Cocha Cashu's vertebrate biomass (759.1 kg/km^2 without white-lipped peccaries) is lower than all four of the other nonhunted sites (Upper and Lower Panagua, Pakitza, and Cumerjali). In fact, both of the nonhunted lowland sites (Cocha Cashu and Pakitza) exhibited a lower aggregate biomass than did the three nonhunted upland sites. We emphasize, however, that our abundance and biomass estimates do not apply to higher elevations of Manu Park (> 600 m asl) nor to the extensive areas of low-phytomass bamboo forests that lie toward the north of the Manu River (*e.g.*, light areas in the upper left of Fig. 1), where we expect the arboreal mammal biomass to be lower.

The inclusion of white-lipped peccaries raises the total vertebrate biomass estimates in the nonhunted sites by an additional 25–141 percent (Table 2). We can only speculate as to the reasons for the recent population recovery (and the original disappearance), but Matsigenka informants have reported that white-lipped peccaries almost completely disappeared from the environs of Yomybato and Tayakome starting in the late 1970s to the early 1980s, and began to return in 1988–1990 (G. Shepard, unpubl. data), although some hunters did manage to kill a few in 1988–1989 (Ohl-Schacherer *et al.* 2007). These dates fit those reported from Cocha Cashu and along the Alto Madre de Dios River (Silman *et al.* 2003). A widespread, simultaneous population decline seems consistent with a hypothesis of epidemic disease and eventual recovery (Fragoso 2004). In support of the disease hypothesis, Matsigenka recall a sudden but more temporary die-back of tapirs in the early 1980s, when seven or more sick individuals or carcasses were found in the forest over the course of several months without any obvious signs of human or animal predation; during about the same time, a number of weak or ill collared peccaries were observed, although their numbers did not decline appreciably (G. Shepard, unpubl. data; Ohl-Schacherer *et al.* 2007). However the Matsigenka observed no such sick individuals or inexplicable carcasses for white-lipped peccaries at the time. Thus the alternative hypothesis of a massive, long-distance migration of white-lipped peccaries is also possible.

LARGE VERTEBRATE RESPONSES TO HUNTING AND FOREST TYPES.—A CCA of the species density dataset produced a roughly *L*-shaped distribution of survey sites (Fig. S1A). Community composition differed significantly (mock ANOVA test, $P = 0.015$) between lowland and upland forest types, with lowland forests characterized by especially higher densities of squirrel monkeys (saimboli), white-fronted capuchins (cebualbi), white-lipped peccaries (tayapeca), brown agoutis (dasyvari), razor-billed curassows (mitutube), and brown (aka tufted) capuchins (cebuapel) (Fig. S1A). The community composition of the two hunted sites (Tayakome and Yomybato) was not formally significantly different from the nonhunted census sites ($P = 0.098$), but did contain higher densities of wood-quails (odontoph, 184% = mean hunted/mean nonhunted density), and Spix's Guan (penejacq, 169%) (as well as gray monk sakis [pithirro, 421%]; Tables 1 and S2; although this species was not included in the dataset; see 'Methods').

CCA of the biomass dataset produced a more T-shaped distribution of survey sites (Fig. S1B). Community biomass composition was not formally significantly different between hunted and nonhunted sites ($P = 0.16$) nor between lowland and upland forest sites ($P = 0.36$). Nonetheless, there were clear effects of hunting on overall biomass. The total censused vertebrate biomass at Yomybato and Tayakome, including white-lipped peccaries, amounted to only 25.8 and 36.2 percent of the average total censused biomass of the nonhunted sites, respectively (Table 2). The higher abundance of white-lipped peccaries in Tayakome accounted for most of the difference between the two Matsigenka settlements (Table 2). Interestingly, some species were more abundant in the hunted sites, especially in Yomybato (Fig. S1B).

TABLE 2. *Vertebrate biomass estimates calculated for those species with reliable* D_{ind} *values (Table 1) and for white-lipped peccaries (*Tayassu pecari*; see 'Methods'). The 'Cocha Cashu JET' column lists biomass estimates from Janson and Emmons (1990) for mammals and Terborgh* et al. *(1990) for birds, and the 'BCI' column lists density and biomass estimates from Barro Colorado Island, Panama (Leigh 1999: Appendix 7.2). The 'CC/CCJET' and 'CC/BCI' columns calculate the ratios of the respective columns.*

	Biomass (kg/km^2)											
Species	Yomybato, hunted	Tayakome, hunted	Upper Panagua	Lower Panagua	Pakitza	Cumerjali	Cocha Cashu	Cocha Cashu JET	BCI (ind/km^2)	CC/CCJET (%)	CC/BCI (%)	Equivalent BCI Species
Primates												
Alouatta sara	3.6	43.2	63.4	59.3	32.8	88.4	44.6	156.0	440 (80)	29	10	*Alouatta palliata*
Ateles chamek	16.6	56.3	331.2	300.8	100.7	353.6	262.3	180.4	5 (1)	145	5246	*Ateles geoffroyi*
Callicebus brunneus	6.6	4.4	15.7	17.0	3.6	10.3	4.9	20.2	–	24		
Cebus albifrons	3.9	5.4	25.7	21.8	49.2	16.0	48.6	75.6	52 (20)	64	94	*Cebus capucinus*
Cebus apella	26.1	13.9	36.0	70.0	70.2	39.7	65.7	93.1		71		
Lagothrix cana	53.0	67.6	92.0	272.4	337.6	237.6	8.4	7.0	–	120		
Pithecia irrorata	4.8	3.3	0.0	0.0	0.0	4.0	0.8	1.8	–	43		
Saguinus fuscicollis	11.5	1.7	11.8	16.6	9.3	13.4	3.9	5.0	2.1 (3)	79	188	*Saguinus geoffroyi*
Saguinus imperator	0.0	0.7	0.0	0.0	0.0	0.0	2.4	4.9		50		
Saimiri boliviensis	0.0	3.0	8.1	22.0	36.0	11.9	37.4	45.1	–	83		
Ungulates												
Mazama spp.[a]	24.1	66.5	79.1	35.7	41.4	115.3	61.4	78	45 (3)	79	136	*Mazama americana*
Pecari tajacu	135.4	65.6	142.4	89.8	39.1	100.7	139.4	140	230 (10)	100	61	*Pecari tajacu*
Tayassu pecari	28.6	150.4	239.2	564.4	1137.7	842.8	389.6	105.5[b]	–	369		
Rodentia												
Dasyprocta variegata	0	4.5	2.7	5.1	5.0	4.7	9.4	20.8	280 (100)	45	3	*Dasyprocta punctata*
Myoprocta pratti	0.3	0.3	1.4	0.3	0.4	1.1	0.7	7.95	–	9		
Sciurus spadiceus	1.4	8.4	22.2	9.2	6.5	8.3	5.4	5	45 (180)	109	12	*Sciurus granatensis*
Birds												
Crypturellus spp.	5.3	3.8	4.8	4.7	8.8	4.6	4.8	15.5		31		
Tinamus spp.	5.5	8.3	6.5	7.4	12.4	27.1	11.7	22.7		51		
Mitu tuberosum	1.5	5.3	14.6	22.1	30.2	19.6	6.8	15.5		44		
Odontoph. gujanensis	35.7	27.6	20.1	19.4	5.5	34.7	6.2	16		39		
Penelope jacquacu	36.1	13.1	21.0	14.2	2.3	30.5	4.8	2.6		183		
Pipile cumanensis	0.0	1.7	0.6	1.7	0.3	1.2	0.8	7		12		
Psophia leucoptera	6.5	16.4	63.2	44.9	17.9	24.5	28.7	13.5		212		
Primate biomass	126.0	199.3	583.8	779.9	639.5	774.9	479.0	589.0		81		
Total biomass without *T. pecari*	378.0	421.0	962.5	1034.5	809.3	1147.1	759.1	933.6		81		
Total biomass with *T. pecari*	406.6	571.4	1201.7	1598.9	1946.9	1989.9	1148.7	1039.1		111		

[a] Mainly *Mazama americana*, but including an unknown small number of *M. gouazoubira* sightings,

[b] Corrected from the original typographical error, '105. < 5.'

DISCUSSION

This study represents the first fully standardized, large-scale series of line-transect surveys of medium- to large-bodied terrestrial vertebrates in Manu Park. The Manu Park ecosystem contains a full complement of forest vertebrate species and, roughly > 85 percent of the park area < 600 m asl (13,851 km^2) has been largely free of persistent hunting for three decades or more. In fact, of all Neotropical forest sites investigated to date, Cocha Cashu Biological Station has been repeatedly portrayed as a prime example of a pristine lowland forest embedded within vast tracts of continuous wilderness areas, and complete with all harvest- and area-sensitive large-bodied vertebrates (Terborgh 1988). This has exposed a debate over the representativeness of a number of ecological processes uncovered at less extensive, more accessible, and more human-modified Neotropical forest sites where several species of large-bodied mammals are locally extinct (*e.g.*, Barro Colorado Island: Wright *et al.* 1994). In the two Panagua census sites (far even from the migration routes of the nomadic Mashco Piro), it is possible that no hunting had taken place for half a century or more before the surveys, even by historical indigenous populations. This provides both an opportunity to characterize an intact vertebrate community and to gauge the effects of subsistence hunting by the two major Matsigenka settlements. Additionally, our standard line-transect census technique allows us to verify previous density estimates at the Cocha Cashu Biological Station.

COCHA CASHU.—A variety of census techniques have been used at Cocha Cashu to estimate the population densities of birds (Robinson & Terborgh 1990, Terborgh *et al.* 1990) and mammals (Terborgh 1983, Janson & Emmons 1990), including live-trapping, nocturnal and diurnal censuses, and intensive single-species observations such as spot-mapping of avian vocalizations and full-day follows of habituated primate groups. Also, most studies at Cashu were restricted to the 600-ha trail system of the main study area and, more specifically, around the permanent research station and the lake (Terborgh *et al.* 1990), whereas our transects covered a much broader area (Fig. 1). The supra-annually inundated mature and young floodplain forest encompassed by this study area may be atypically productive, compared with other parts of Manu Park, for reasons related to water stress during the dry season and soil fertility (Mazer 1996). For example, population densities of howler monkeys and other arboreal folivores across Amazonia decline nonlinearly with distance to rivers and alluvial floodplains (Peres 1997b), a pattern that runs against what would be expected if howler densities were primarily driven by hunting pressure. Previous density estimates at Cashu (Saavedra 1984) might therefore be expected to differ from those reported here. The most obvious disparities between this study and the historical estimates at Cashu are the lower biomass estimates for red howler monkey (*Alouatta sara*) and brown titi monkey (*Callicebus brunneus*), for which previous estimates are 3.5 and 4.1 times higher, respectively (Table 2). Likely explanations are that brown titi monkeys are small and secretive and that howler monkeys are often inactive and high in the canopy. They may therefore be easily overlooked during strip censuses, but can be counted when groups are followed individually. Otherwise, there is good overall correspondence between our density estimates and those obtained previously at Cocha Cashu. Omitting only white-lipped peccaries, the Pearson correlation coefficient between our biomass results and those of Janson and Emmons (1990) is 0.86 ($P < 0.001$; Table 2).

As already stated, despite the fact that lowland forest soils, such as at the Cocha Cashu site, are more fertile (Mazer 1996, Ohl *et al.* 2007), our results showed a lower aggregate biomass in Cocha Cashu and Pakitza than in the nonhunted upland sites, suggesting that most of the core area of Manu Park, which is primarily comprised of upland forest, has a vertebrate biomass density similar to or higher than that of Cocha Cashu.

MANU VS. OTHER AREAS.—Manu Park safeguards some of the most species-rich and highest biomass of mid- to large-bodied forest vertebrate assemblages in any Neotropical forest, confirming and even surpassing earlier surveys based on a much smaller sampling effort restricted to Cocha Cashu (Emmons 1984b). This is clearly the case for both terrestrial and arboreal mammals in nonhunted portions of Manu Park that are well beyond the hunting catchment areas of the two major Matsigenka settlements. For example, the five nonhunted mature floodplain and upland forests surveyed (Cumerjali, Lower Panagua, Upper Panagua, and Pakitza) were within the top 10 aggregate primate biomass estimates for any of 148 forest sites surveyed to date throughout lowland Amazonia and the Guianan Shields (C.A. Peres, unpubl. data); even the lowest estimate obtained from these five sites is above the 95th percentile (based on an empirical distribution function of all Amazonian primate surveys). Furthermore, Lower Panagua, Cumerjali, and Pakitza had the highest primate biomass levels recorded to date, except for a seasonally flooded Pleistocene *várzea* forest along the Rio Juruá, Brazil, that is also subjected to little or no hunting (Boa Esperança: Peres 1997a).

Studies have indicated a strong correlation between soil fertility and vertebrate abundance in Amazonian forests (Peres 2000, 2008). Oligotrophic forests, such as those found in much of Central Amazonia and the Guianan Shield region tend to support a low density of large vertebrates, but not necessarily a lower species richness. However, lower population densities increase the probability that any given species will be overlooked for a given amount of census effort. That we repeatedly recorded 12 of the 14 primate species known to occur in Manu (all except the rare Goeldi's monkey and the secretive pygmy marmoset, both of which are extreme forest habitat specialists), is a good example of the contrast between Manu Park and less nutrient-rich Amazonian forests. The exceptionally high habitat productivity of Manu Park for arboreal mammals is underscored by the fact that both of the largest primate species (woolly and spider monkeys) were frequently represented in large numbers, co-occurred microsympatrically, and were often observed in relatively stable mixed-species groups. This is highly unusual at other Amazonian sites where these genera co-occur (Iwanaga & Ferrari 2002; C.A. Peres, unpubl. data).

We also revise previous faunal density comparisons between Manu (Cocha Cashu Biological Station) and Barro Colorado Island in Panama (Terborgh 1988, Wright *et al.* 1994, Leigh 1999). Compared with Manu, Barro Colorado Island has a much lower biomass of spider monkeys (and large mammals with large spatial requirements such as, woolly monkeys and white-lipped peccaries), but a much higher biomass of large rodents (*Dasyprocta* and *Agouti*), howler monkeys (*Alouatta*), and sloths (*Bradypus* and *Choloepus*) (Table 2; Leigh 1999: Appendix 7.2). In fact, both sloth genera, the largest contributors to mammal biomass at Barro Colorado Island (1490 kg/km^2 for *Bradypus variegatus* alone), were never recorded in our censuses, nor was a single individual detected on any other occasion inside Manu Park during the entire fieldwork period, which is unexpected, even considering the difficulty of detecting sloths in the forest (sub)canopy. This is consistent with a hunting study carried out inside the Manu Park (Ohl-Schacherer *et al.* 2007), where no sloths were recorded in a list of 2089 animals killed during a 1-yr period by Matsigenka hunters. Yet this list included many prey items (birds and mammals) smaller than either of the two sloth species occurring in Manu Park. The apparent low abundance of sloths in both upland and lowland forest sites is in marked contrast with Amazonian seasonally inundated (*várzea*) forests with a sustained annual flood pulse, where sloths represent a major part of the arboreal mammal biomass (Peres 1999a). In short, Barro Colorado Island is characterized by high abundances of seed predators and arboreal folivores (Eisenberg & Thorington 1973) and relatively low abundances of generalist frugivores that specialize on mature fruit pulp. Given that both small and large predators were detected regularly in all Manu census transects (see also Emmons 1984a, Janson & Emmons 1990), it is tempting to explain these differences, which were consistent across both nonhunted and hunted sites, by invoking stronger top-down control (Terborgh *et al.* 2001). However, bottom-up mechanisms are also likely important, considering the high production of fruits and seeds in Manu (Terborgh 1983) and other significant differences in the resource base available to vertebrate consumers at these forest sites.

EFFECTS OF HUNTING.—The aggregate large vertebrate biomass was considerably higher in nonhunted forest sites, compared with the sites within the core hunting catchment of the two main Matsigenka settlements in Manu Park. This is consistent with comparisons of hunted and nonhunted sites within and outside forest catchments harvested by a wide range of subsistence hunters in Amazonia (*e.g.*, Hill *et al.* 1997, Mena *et al.* 2000, Peres 2000; see meta-analysis in Peres & Palacios 2007). Moreover, these results are unlikely to be largely driven by differences in forest productivity because nonhunted, upland forest sites sustained an aggregate game vertebrate biomass 2–4+-fold higher than that of the hunted sites, which are also located in upland forest areas (Fig. 1). For key harvest-sensitive game species, such as spider monkeys, population densities in hunted sites were up to 21 times lower in hunted sites compared with nonhunted sites of the same forest type. A recent analysis of game offtake by the Matsigenka using the Robinson and Redford production index (Ohl-Schacherer *et al.* 2007), which is known to flag up only severe cases of overhunting (Milner-Gulland & Akçakaya 2001), estimated that five mammal and gamebird species were being exploited unsustainably within the hunting zones of these two settlements: spider monkeys, woolly monkeys, razor-billed curassows, Spix's guan, and white-lipped peccaries. Nonetheless, populations of all five species still occur within both hunting zones, and Spix's guan exhibits abundances that exceed those in nonhunted areas (Tables 1, 2 and S2). Recent analyses (Levi *et al.* 2009) find that because Matsigenka hunters use bow-and-arrow technology, there has not been enough time since settlement founding to extirpate the large-primate populations within the settlements' 10 km-radius hunting zones, which are also being supplemented by immigration from nonhunted source areas (Ohl-Schacherer *et al.* 2007).

In addition, a few vertebrate species were more abundant in one or both of the hunted sites, including Spix's guan (*P. jacquacu*), marbled wood quail (*O. gujanensis*), collared peccary (*P. tajacu*), saddle-back tamarin (*S. fuscicollis*), and tinamous (primarily *Crypturellus* spp.) or did not show clear decreases (*e.g.*, red brocket deer, *M. americana*) (Tables 1, 2 and S2; Fig. S1A and B). One possible explanation is that these species have been released from competition or predation by species that are directly or indirectly suppressed in hunted sites, thereby exhibiting partial density compensation (Peres & Dolman 2000). It is also possible that the habitat matrix created by slash-and-burn agriculture near the Matsigenka settlements (Ohl *et al.* 2007) favors one or more of these species. For instance, increased abundance of Spix's guan has also been reported by Raez-Luna (2001) around the Piro settlement of Diamante, just outside Manu Park. Such species have been referred to as 'anthropogenic fauna' (Naughton-Treves *et al.* 2003) and are typically characterized by high intrinsic population growth rates (Bodmer *et al.* 1997). A final reason that would explain the higher densities of some of those species in the Matsigenka catchments is their low importance in the 'hunter's menu' (Jerozolimski & Peres 2003), especially considering the high abundance of more desirable target species. This is the case of at least several species < 1 kg, including *Saguinus* spp., *O. gujanensis,* and *Crypturellus* spp.

In summary, our extensive line-transect surveys document that Manu National Park contains some of the highest densities of mid- to large-bodied terrestrial vertebrates ever recorded in Neotropical forests, confirming and even surpassing previous estimates made at Cocha Cashu Biological Station. We detect the effects of hunting by Matsigenka indigenous people only in the hunting zones surrounding Matsigenka settlements (as predicted in Levi *et al.* 2009). Manu Park's vertebrate assemblage therefore provides a snapshot of how a nutrient-rich Neotropical forest 'should be'. Compared with the intensively studied, artificially created Barro Colorado Island research site, midsized seed predators and arboreal folivores in Manu are relatively rare, and arboreal frugivores specializing on mature fruit pulp are abundant. The impact of such a qualitative shift in the vertebrate community on the dynamics of plant regeneration, and therefore, on our understanding of tropical plant ecology, must be profound.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Details of census sites and transects.*

TABLE S2. *Species, sighting rates, and population density estimates at the different sites censused in Manu National Park. ER: Encounter rate (group sightings/10 km walked);* D_{ind}*: Density of individuals (/km*^{2}*);* D_{clt} *= Density of clusters (/km*^{2}*); CV = coefficient of variance of estimates; U = upland, terra firme forest; L = lowland, floodplain forest. Densities not calculated for species with low sample sizes (see text). Tayakome and Yomybato are the two hunted sites. White-lipped peccary population density estimates derived on the basis of a global model stratified by site-specific encounter rates, in which sampling units are defined as small clusters of peccaries (*N *= 93) sighted from the transect.*

FIGURE S1. Constrained correspondence analysis of animal species (A) density and (B) biomass estimates in the seven forest sites censused.

FIGURE S2. Example frequency distribution of perpendicular distances and the best-fit detection function selected, based on the data obtained for razor-billed curassow in Manu National Park, Peru.

APPENDIX S1. (A) Description of the Perpendicular Distance (PD) estimation procedure; (B) Pre-ANOVAS; (C) Minimum number of detections.

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TABLE S1. *Details of census sites and transects.*

Site	Location (UTM, 19L Easting)	Location (UTM, 19L Northing)	Number of transects	Forest type	Hunting status	Census months	Transect length (km)	Total km censused per transect	Total km censused (morning)
Pakitza	251537	8678799	2	Lowland	Not hunted	30 JAN, 1–2 FEB, 8 MAR, 15–21 JUN	4499	79.6	162.2 (87.77)
							4575	82.7	
							–	–	
Lower Panagua	244408	8674864	3	Upland	Not hunted	10–23 FEB	4499	76.4	234.5 (130.1)
							4499	77.5	
							4499	80.6	
Upper Panagua	226770	8676177	3	Upland	Not hunted	8–17 JAN	4499	42.9	170.0 (108.48)
							4651	52.9	
							5032	74.3	
Cocha Cashu	237881	8685222	3	Lowland	Not hunted	21–23 JAN, 25–27 FEB, 23–30 JUN	5002	82.6	218.2 (118.4)
							3660	55.2	
							4575	80.4	
Cumerjali	213472	8687130	3	Upland	Not	17–31 MAR, 1	4499	80	226.8

					hunted	APR	4499	84.2	(130.7)
							4499	62.6	
Tayakome	210528	8701744	3	Upland	Hunted	15–27 JUL	4499	85.4	235.2 (125.7)
							4697	79.8	
							4514	70	
Yomybato	181863	8694139	3	Upland	Hunted	11–28 APR	4499	79.8	248.0 (137.5)
							4499	87.3	
							4499	75	

		Yomybato$_{Hunted,}$ U				Tayakome$_{Hunted,}$ U				Upper Panagua, U				Lower Panagua, U				Pakitza, L				Cumerjali, U				Cocha Cashu, L			
Common Names	Taxa	ER	D_{ind}	D_{clt}	CV	ER	D_{ind}	D_{clt}	CV	ER	D_{ind}	D_{clt}	CV	ER	D_{ind}	D_{clt}	CV	ER	D_{ind}	D_{clt}	CV	ER	D_{ind}	D_{clt}	CV	ER	D_{ind}	D_{grp}	CV
Primates																													
Black-capped squirrel monkey	*Saimiri boliviensis*	*0*	-	-	-	*0.04*	4	*0.3*	*18.5*	*0.24*	10.8	*0.8*	*18.5*	*0.51*	29.3	*2.2*	*18.5*	*1.08*	47.9	*2.7*	*18.5*	*0.4*	15.8	*1.2*	*18.5*	*1.01*	49.7	*1.8*	*18.5*
Brown-mantled tamarin	*Saguinus fuscicollis*	*2.02*	37	*7.2*	*6*	*0.24*	5.3	*1*	*6*	*2.65*	37.8	*7.3*	*6*	*2.38*	53.3	*8.3*	*6*	*1.44*	29.9	*4*	*6*	*2.3*	43	*8.3*	*6*	*0.51*	12.7	*1.8*	*6*
Emperor tamarin	*Saguinus imperator*	*0*	-	-	-	*0.32*	1.6	*0.4*	*42.3*	*0*	-	-	-	*0*	-	-	-	*0*	-	-	-	*0*		-	-	*0.25*	6	*1.5*	*42.3*
Brown titi	*Callicebus bruneus*[3]	*0.51*	7.8	*2*	*12.1*	*0.26*	5.2	*1.3*	*12.1*	*2.46*	18.6	*4.7*	*12.1*	*1.71*	20.2	*5.1*	*12.1*	*0.19*	4.3	*1.1*	*12.1*	*0.61*	12.3	*3.1*	*12.1*	*0.25*	5.8	*1.5*	*12.1*
Gray monk saki	*Pithecia irrorata*[5]	*0.58*	4.8	*1.1*	*22*	*0.16*	1.9	*0.43*	*22*	*0*	-	-	-	*0*	-	-	-	*0*	-	-	-	*0.23*	2.3	*0.52*	*22*	*0.09*	1.1	*0.25*	*22*
Brown capuchin	*Cebus apella*	*0.97*	11.2	*2.6*	*5.9*	*0.95*	6	*2.6*	*5.9*	*0.94*	15.5	*2.8*	*5.9*	*1.11*	30.1	*5.1*	*5.9*	*2.16*	30.2	*5.8*	*5.9*	*1.32*	17.1	*3.6*	*5.9*	*2.03*	28.2	*5.4*	*5.9*
White-fronted capuchin	*Cebus albifrons*	*0.22*	1.8	*0.5*	*5.8*	*0.34*	2.5	*0.54*	*5.8*	*0.76*	11.9	*1.6*	*5.8*	*0.26*	10.1	*0.8*	*5.8*	*1.48*	22.8	*3.2*	*5.8*	*0.61*	7.4	*1.4*	*5.8*	*1.94*	22.5	*4.4*	*5.8*
Bolivian red howler	*Alouatta sara*[1]	*0.07*	0.7	*0.16*	*14*	*1.43*	8.3	*1.7*	*14*	*1.7*	12.2	*2.6*	*14*	*1.41*	11.4	*2.4*	*14*	*0.36*	6.3	*1.3*	*14*	*1.15*	17	*3.5*	*14*	*1.01*	8.6	*1.8*	*14*
Gray woolly monkey	*Lagothrix cana*[4]	*1.29*	7.6	*2*	*4.2*	*1.99*	9.7	*2.6*	*4.2*	*0.85*	13.2	*1.3*	*4.2*	*1.56*	39.1	*5.7*	*4.2*	*6.12*	48.5	*8.2*	*4.2*	*2.51*	34.1	*5.7*	*4.2*	*0*	1.2	*0.2*	*4.2*
Peruvian spider monkey	*Ateles chamek*[2]	*0.43*	2.3	*0.51*	*3.1*	*2.15*	7.8	*2.2*	*3.1*	*6.43*	45.9	*8.7*	*3.1*	*4.76*	41.7	*6.4*	*3.1*	*2.64*	14	*3.9*	*3.1*	*8.65*	49	*8.9*	*3.1*	*5.15*	36.3	*8.6*	*3.1*
Ungulates																													
South American red & gray brocket deer	*Mazama spp.*[6]	0.14	1	0.98	72.6	0.32	2.7	2.16	52.6	0.57	3.21	3.21	47.6	0.22	1.45	1.45	47.6	0.25	1.68	1.68	52.6	0.69	4.68	4.68	37.2	0.51	2.49	2.49	39
Collared peccary	*Pecari tajacu*[7]	0.32	7.8	1.95	38.7	0.24	3.78	1.03	52.4	0.57	8.2	3.21	36.8	0.26	5.17	1.55	43.7	0.24	2.25	0.75	72.4	0.38	5.8	2.32	47.4	0.5	8.03	3.06	34
White-lipped peccary	*Tayassu pecari*	0.04	1.1	0.07	100	0.2	5.8	0.36	44.7	0.3	9.2	0.57	46.3	0.8	21.7	1.34	30.1	1.6	43.8	2.7	22.9	1.1	32.4	2	22.6	0.6	15	0.93	31.2
South American tapir	*Tapirus terrestris*	0	-	-	-	0.08	-	-	-	0	-	-	-	0.04	-	-	-	0	-	-	-	0	-	-	-	0.08	-	-	-
Carnivores																													
Tayra	*Eira barbara*	0	-	-	-	0.04	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0.05	-	-	-
Bush dog	*Speothos venaticus*	0	-	-	-	0	-	-	-	0	-	-	-	0.07	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-

Jaguar	*Panthera onca*	0	-	-	-	0.03	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0.09	-	-	-	0.05	-	-	-
Ocelot	*Leopardus pardalis*	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0.06	-	-	-	0	-	-	-	0	-	-	-
South American coati	*Nasua nasua*	0.04	-	-	-	0	-	-	-	0.06	-	-	-	0	-	-	-	0	-	-	-	0.04	-	-	-	0.05	-	-	-
Giant otter	*Pteronura brasiliensis*	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0.05	-	-	-
Xenarthra																													
Southern Tamandua	*Tamandua tetradactyla*	-	-	-	-	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	-
Giant Anteater	*Myrmecophaga tridactyla*	0	-	-	-	0	-	-	-	0.06	-	-	-	0	-	-	-	0.06	-	-	-	0.09	-	-	-	0	-	-	-
Rodentia																													
Brown agouti	*Dasyprocta variegata*	0	-	-	-	0.4	1.64	1.44	37.3	0.28	0.99	0.99	51.4	0.45	1.88	1.88	42.5	0.43	1.83	1.57	42.5	0.31	1.72	1.29	51.4	0.84	3.47	3.21	35.4
Green acouchy	*Myoprocta pratti*	0.07	0.5	0.5	105	0.08	0.53	0.53	105	0.19	2.2	2.2	66.1	0.04	0.53	0.53	105	0.12	0.55	0.55	105	0.23	1.65	1.65	66.1	0.92	1.14	1.14	77.7
Squirrel spp.	*Sciurus spp.*[8]	0.22	2.49	2.49	59.3	1.35	15	11.9	30.9	1.42	39.7	16.3	29.2	1.26	16.4	12.8	29.2	0.84	11.6	8.29	43	1.22	14.8	14.1	28.5	1.01	9.72	9.72	34.4
Amazon dwarf squirrel	*Microsciurus flaviventer*[9]	0.04	-	-	-	0.04	-	-	-	0.06	-	-	-	0	-	-	-	0.06	-	-	-	0	-	-	-	0	-	-	-
Lagomorpha																													
Tapeti	*Sylvilagus brasiliensis*	0.07	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-
Birds																													
Small Tinamou spp.	*Crypturellus spp.*[10]	1.3	17.7	16.6	20.1	0.9	12.8	10.2	25.2	1.04	16.1	11	28.2	0.98	15.9	13.1	22.7	1.98	29.5	24.7	20.3	1.15	15.3	13.5	22.7	1.18	16	14.6	29.1
Large Tinamou spp.	*Tinamus spp.*[11]	0.51	5.52	5.52	31.4	0.8	8.27	8.27	27.2	0.59	6.46	5.38	37.5	0.47	7.32	5.37	32.6	0.96	12.4	9.61	39.8	1.54	26.9	17.5	25.6	1.1	11.6	11.6	31.4
Razor-billed Curassow	*Mitu tuberosum*	0.07	0.62	0.31	100	0.4	2.12	1.7	45.4	1.61	5.9	4.01	26.1	1.63	8.9	6.54	18.3	1.44	12.2	4.74	24.7	1.19	7.89	5.07	20.7	0.51	2.73	1.76	34.2

Marbled Wood-quail	*Odontophorus gujanensis*	0.94	89.3	15.5	25.2	1.11	69.1	14.9	26.2	0.94	50.2	10.9	37.5	0.67	48.6	9.4	31.5	0.19	13.6	3.41	59.1	0.92	86.8	15.5	32.7	0.28	15.5	4.22	46.5
Spix's Guan	*Penelope jacquacu*	1.73	34.7	10.5	22.6	0.72	12.6	4.12	26.8	1.42	20.2	7.48	23.9	1.04	13.7	6.2	22.6	0.19	2.24	1.12	58.5	1.84	29.3	9.87	19.1	0.51	4.58	3.05	31.7
Blue-throated Piping-guan	*Pipile cumanensis*	0	0	-	-	0.24	1.55	0.52	64.5	0.06	0.53	0.24	104	0.21	1.55	0.86	53.2	0.12	0.25	0.25	104	0.09	1.07	0.36	76.3	0.18	0.74	0.37	76.3
Pale-winged Trumpeter	*Psophia leucoptera*	0.29	5.42	1	42.1	0.4	13.7	1.65	45.9	2.18	52.7	7.08	21.2	1.24	37.4	5.14	21.2	0.74	15	3.08	30.7	0.79	20.4	3.29	25.7	0.76	23.9	3.16	34.9
Speckled Chachalaca	*Ortalis guttata*	0	-	-	-	0	-	-	-	0.06	-	-	-	0	-	-	-	0.06	-	-	-	0	-	-	-	0	-	-	-
Reptiles																													
Yellow-footed tortoise	*Geochelone denticulata*	0	-	-	-	0	-	-	-	0.06	-	-	-	0.13	-	-	-	0.06	-	-	-	0.09	-	-	-	0	-	-	-

[1]= *A. seniculus*
[2]= *A. paniscus* and *A. belzebuth*
[3]= *C. moloch*
[4]= *L. lagotricha*
[5]= *P. monachus*
[6]= Mainly *Mazama americana*, but including an unknown small number of *M. gouazoubira* sightings,
[7]= *Tayassu tajacu*
[8]= *S. spadiceus and S.sanborni*
[9] = *M. flavescens*
[10] = *C. cinereus, C.soui, C.bartletti, C.variegatus, C.atrocapillus, C.undulatus (and C.strigulosus (Walker et al.2006))*
[11] = *T.tao, T.major and T.guttatus*

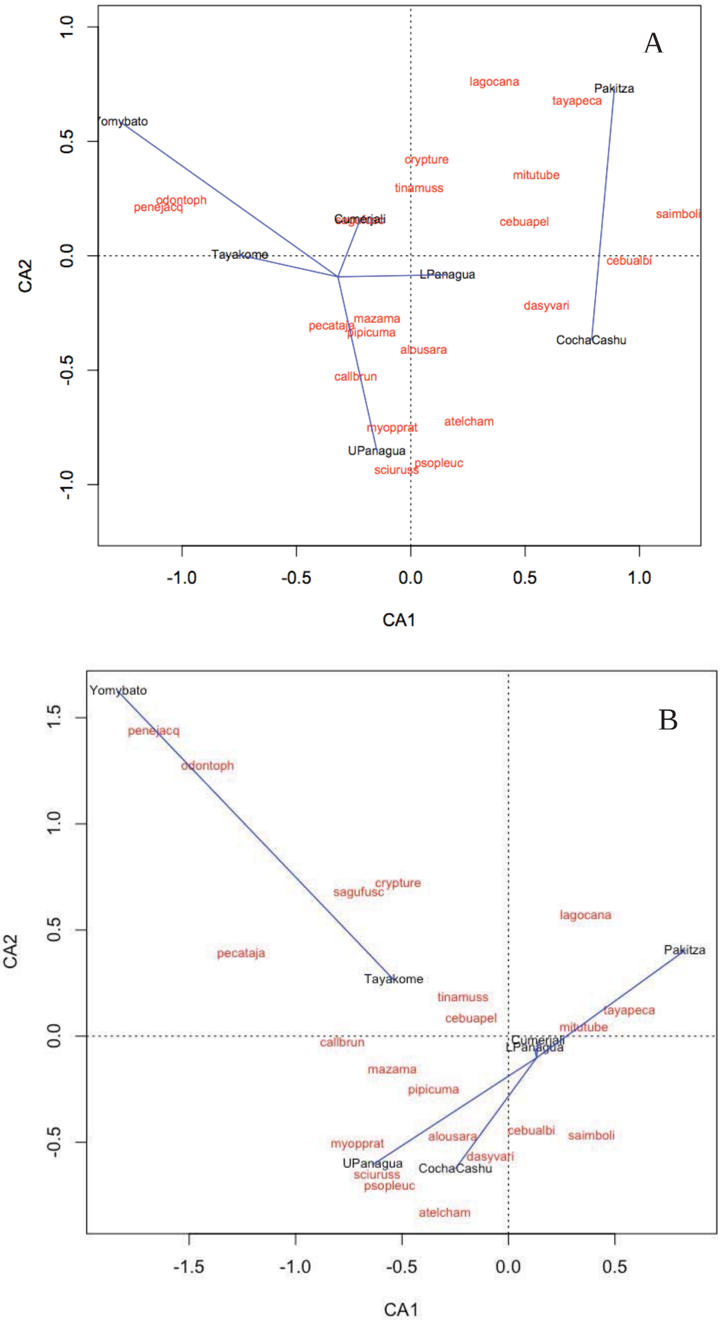

FIGURE S1. Constrained correspondence analysis of animal species (A) density and (B) biomass estimates in the seven forest sites censused. The *ordispider* function in *vegan* (see Methods) is used to connect sites by forest type. See text for statistical details. Species codes combine the first four letters from the genus name and species epithet (see Tables 1 and S2).

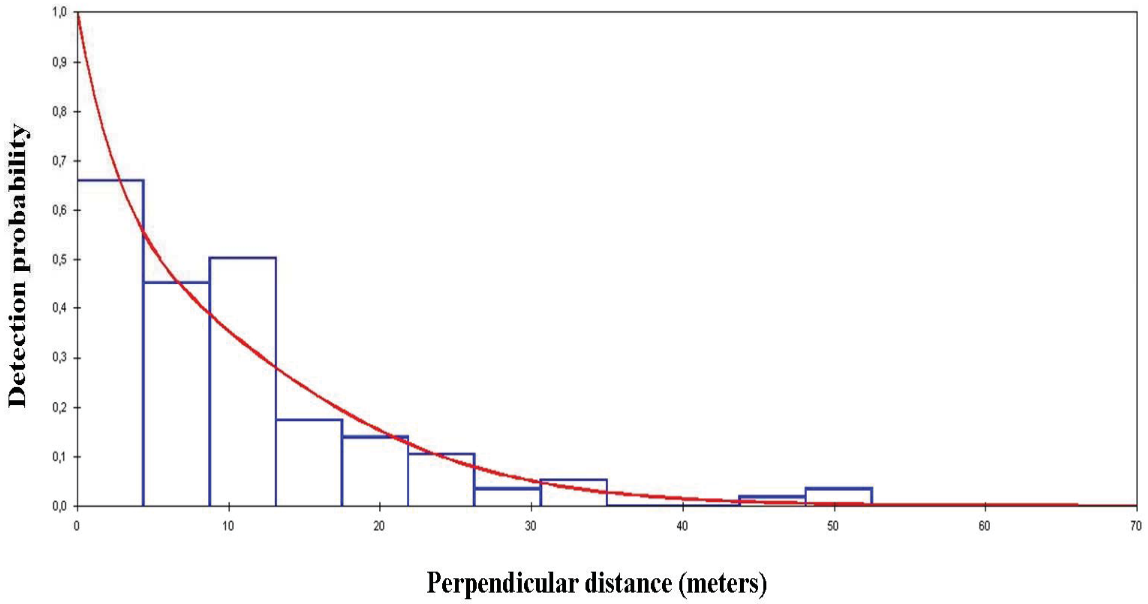

FIGURE S2. Example frequency distribution of perpendicular distances (blue bars) and the best-fit detection function selected (red line), based on the data obtained for razor-billed curassow (*Mitu tuberosa*) in Manu National Park, Peru.

APPENDIX 1

a) Description of the Perpendicular Distance (PD) estimation procedure

Distance sampling was used to estimate the densities of the most abundant species censused in this study. Following standard guidelines (Buckland *et al*. 1993) to estimate the density of each population in the study sites, we first recorded, for all animals detected along the transects during our standardized surveys (Peres 1999), the perpendicular distance (PD) to each individual (or group). Based on the frequency distribution of all PD data recorded, we obtained a detection function that provides the probability of detecting an object based on the distance that this object is from the transect line (Fig. S2). The detection function is obtained by means of a selection of a model that best represents the frequency distribution of those PDs. To increase the robustness of each model estimate (Buckland *et al*. 1993), we proceeded by fitting each PD distribution using both truncated and untruncated data. In most cases, truncation of observations corresponded to the most evident high-value outliers, usually fewer than 10 percent of the detection events obtained in the field.

b) Pre-ANOVAs

To allow pooling of observations across all sampling sites and thus to increase the representativeness of the detection functions obtained, it was necessary to test for differences in the intrinsic detectability of any given species occurring at different sites surveyed within Manu National Park. These differences could result from idiosyncrasies in, for example, forest structure or in the terrain of each one of those sites. We used ANOVAs to detect if mean PDs differed significantly across sites, using the threshold of formal significance, $P > 0.05$, to accept the null hypothesis of no significant difference. Note that we did not inflate *P*-values to correct for table-wide comparisons, further underlining the lack of significant differences. (*P*-values: range = 0.051–0.951, mean ± SD = 0.299 ± 0.25). Another way of viewing these data is that each non-significant *P*-value increases confidence that overall detectability does not differ amongst forest sites and that, therefore, one should err on the side of pooling PDs.

c) Minimum number of detections

A minimum number of detections is required to provide reliable density estimates, which is the number of independent detection events that is sufficiently high to provide well-defined frequency distributions and, thus, reliable detection functions (Fig. S2), as defined by the number of parameters in detection functions and small coefficients of variation (preferably ≤ 0.4). As a rule of thumb, samples with 40 or more detection events are sufficient to achieve this (Buckland *et al*. 1993), but reliable detection functions can be fitted with fewer, if well behaved. In this study, 17 of the 22 detection functions were based on sample sizes > 40 detection events (range: $N = 13$–421 events, mean ± SD = 101.7 events ± 87.9), and all could be fitted with detection functions. The five low sample-size species are listed in the main text.

PAPER III

Paper III describes the composition of the medium- and large-bodied mammal community found at three of the most important protected areas of the Caatinga, the largest xeric scrub and dry forest biome of South America. Moreover, the study evaluates the influences of rural populations living in the surroundings of these PAs and of environmental factors on the occupancy of six medium- and large-sized mammals, including four carnivore species.

Photo: W. Endo

Anthropogenic and Environmental Correlates of Medium- and Large-Bodied Mammal Occupancy in Protected Areas of the Brazilian Caatinga

Correlates of mammal occupancy in the Caatinga

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Abstract

The semi-arid Caatinga is a unique South American biome harboring a large number of endemic species and accounting for 18% of Brazil’s territory. Yet the Caatinga has succumbed to extensive natural habitat loss and wildlife population declines due to a myriad of threats, including widespread livestock husbandry within its boundaries. The Caatinga is also the least protected of all major Brazilian biomes in terms of total number of reserves and proportional area, and quantitative studies are needed to evaluate the effectiveness of its protected areas. We conducted camera-trap surveys in three of the main reserves of the Caatinga biome to assess the patterns of community composition and occupancy, in relation to environmental and anthropogenic variables, of six large terrestrial mammal species, including four carnivores, one ungulate, and one large rodent. A total of 2,710 camera-trapping days were conducted across the study sites showing varying patterns of species occupancy, which were primarily related to the proportion of forest area, understory density, and elevation. Our results also showed that, with the exception of the two most resilient species (black-rumped agouti and crab-eating fox), these species exhibit higher occupancy rates at sites farther from the reserve edge and/or with a lower incidence of cattle, thereby indicating their vulnerability to human influences. These results and other factors, such as the heavy use of free-ranging cattle within even the most strictly protected area surveyed here, suggest the need to improve reserve management to mitigate potential threats related to the growing impacts of human activities within Caatinga reserves.

Introduction

With a remarkable plant and animal diversity, South American countries, and Brazil in particular, have put in place a conservation strategy to markedly reduce biodiversity loss, including a steep escalation in the number and combined area of existing protected areas. With a total of 1,864 reserves encompassing an area of 228 million ha, Brazil now hosts the largest national protected area (PA) system worldwide [1,2]. However, the proportional reserve allocation to different biomes is highly uneven. For example, 47% of Brazilian Amazonia is now encompassed by a network of reserves and indigenous territories [3], whereas only less than 7% of the remaining semi-arid Caatinga biome of approximately 832,000 km^2 across 10 Brazilian states is officially protected [4]. This is also the least investigated of all major Brazilian biomes [5]. Despite its highly neglected status, the Caatinga is a unique biome accounting for 18% of Brazil's territory, and harboring a large number of endemic plant, invertebrate and vertebrate species [5]. With more than 25 million people living within the boundaries of this biome, it is also one of the world's most densely populated semi-arid regions, facing pervasive overexploitation of natural resources and increasing degradation of its ecosystems [6, 7]. There is therefore an urgent need to better understand the current pressures on this biome to both inform conservation planning and protect its remaining biodiversity.

Brazilian PAs are being gradually degraded by a myriad of human influences, which are likely to weaken the effectiveness of PAs in safeguarding the country's biodiversity [1,8,9]. Among such threats, the impact of domestic livestock on natural vegetation is an example of a growing threat yet to be properly assessed. Brazil contains a burgeoning population of 213 million head of bovine cattle, and the largest anthropogenic pasture area and commercial beef cattle stock of any country

[10,11], leading to major impacts on natural ecosystems, particularly forest areas [12,13]. In fact, all major Brazilian biomes are negatively affected by livestock ranching at varying levels of intensity [4,14-17]. Large livestock have significant impacts on plant and wildlife populations through a diverse set of synergistic mechanisms, even in regions where cattle management does not require prior landscape transformation through intensive conversion of natural scrub and forest vegetation. Cattle grazing, trampling, and soil compaction and erosion, for example, alter soil properties, hydrologic regimes and vegetation structure and composition [18-21]. Free-ranging cattle also directly affect wild animal populations through competition between cattle and native herbivores for forage, water and other resources [22-24], transmission of zoonotic diseases [25-27], and by increasing hunting pressure [28-31]. Livestock use of Caatinga rangelands, currently estimated at ~33.7 million animals consisting mainly of bovine cattle, followed by sheep and goats [10, S1 Fig.], is therefore an ubiquitous conservation concern, even within formal strictly-protected areas from which legally mandated cattle exclusion is rarely enforced [4].

Medium- and large-sized mammals are among the taxonomic groups that arguably benefits the most from the creation of PAs due to their extensive spatial requirements and high vulnerability to anthropogenic influences, such as habitat loss and overhunting [32,33]. With one-fourth of all species currently listed as threatened [34], carnivores are particularly seen as a mammalian order of high conservation concern. Because of their role as apex predators, changes in carnivore populations are likely to cascade through other co-occurring species potentially degrading the long-term structure of entire ecosystems [35-37]. Declines in the abundance of apex carnivores, for example, are expected to trigger top-down trophic cascades, often releasing smaller guild members from predation and/or competition, thereby elevating abundances of mesocarnivore populations [38,39]. At lower trophic levels, this may promote co-declines in the abundance of smaller prey populations. Such effects, however, are hardly detected in observational studies due to the high complexity of inter-specific interactions and environmental gradients [38,40,41].

Despite the poor overall coverage of PAs within the Caatinga biome, and the pervasive threat of cattle ranching permeating into xeric and thorn scrub rangelands, the current effectiveness of existing reserves and the effects of free-ranging cattle on native mammal populations remains poorly understood. Here, we assess the patterns of medium- and large- sized terrestrial mammal occupancy, namely meso- and large carnivore populations and their potential prey, at three well-established federal PAs subjected to different levels of protection. All of these PAs are encompassed by the Caatinga biome, two of which represent the largest Caatinga PAs and are widely considered to be extremely important to the conservation of this biome [4,42]. Accordingly, we investigate the potential effects of human activities and baseline environmental variables on the occupancy of midsized to large-bodied mammals, and their implications to their conservation and management of Caatinga PAs.

Materials and Methods

Study area

This study was carried out in northeastern Brazil, within the states of Bahia and Piauí (8^o26'S, 42^o45'W and 14^o08'S, 38^o26'W; Fig. 1). This region has a semi-arid climate, with mean annual rainfall between 500 and 750 mm, and an elevational range between 200m and 800m a.s.l. Three major strictly PAs of the Brazilian Caatinga were surveyed during this study (Fig. 1): the 91,849 ha Serra da Capivara National Park (hereafter, SCNP); the 104,843 ha Raso da Catarina Ecological Station (hereafter, RCES); and the 11,216 ha Contendas do Sincorá National Forest (hereafter, CSNF). These reserves represent different PA categories in terms of nominal levels of protection and management restrictions. Ecological Stations have one of the most restrictive levels of protection in Brazil, with no human activities allowed other than scientific research and environmental education. Natural resource use restrictions in National Parks are more relaxed, as they permit low-impact ecotourism but no exploitative activities. Finally, National Forests can be legally subjected to renewable resource extraction, provided that these activities are expected to be defined as sustainable [43].

Fig. 1. Map of the study area showing the location of the three protected areas surveyed. a) Serra da Capivara National Park (SCNP), b) Contendas do Sincorá National Forest (CSNF), and c) Raso da Catarina Ecological Station (RCES). The map also depicts the 832,000-km^2 Caatinga biome within the drought polygon of northeast Brazil (shaded area). Yellow dots indicate camera trap survey sites within the three reserves.

All three reserves are encompassed by the Caatinga *sensu lato* biome, with dry dense shrubby to woodland Caatinga vegetation types covering most of their areas, even though smaller patches of open shrubland Caatinga may be found, especially at SCNP.

Camera trapping

The surveys were conducted between 7 May and 11 December 2012 using motion sensitive camera traps (Tigrinus cameras – www.tigrinus.com.br) installed at 89 trapping stations distributed across all three reserves (SCNP = 41, RCES = 23, CSNF = 25), with a mean distance of 822.2 ± SD 286.6 m between neighboring stations. CTs were set up at c. 50 cm above ground and all CT stations were unbaited, and set along trails which were not transited by humans. Camera traps were also deployed in a manner to cover different portions of the reserves, and represent the variation in habitat types and distance to reserve boundaries. Due to logistic constraints and restrictions imposed by reserve managers, most locations were used in pre-existing trails although some previously selected locations were excluded from our surveys.

Each camera was inspected every 15 days for battery and memory card replacement and data collecting. For each animal photographed, we extracted the date, time and species identification. Multiple records of the same species photographed at the same site were only considered independent if the interval between two consecutive records was longer than 30 minutes.

Predictors of species occupancy

Notwithstanding the relatively high diversity of large- and medium-sized mammal species expected to occur at the surveyed sites [44], we restricted our analyses to six species (S2 Fig.): jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus* *pardalis*), crab-eating fox (*Cerdocyon thous*), gray brocket deer (*Mazama gouazoubira*) and black-rumped agouti (*Dasyprocta prymnolopha*). With the exception of jaguar, all of these species were relatively abundant in the surveyed areas, thereby providing the minimum necessary number of detections for parameter estimation.

Our first hypothesis was that mammal species occupancy would be favored in areas subjected to lower influence from human activities, and that areas far removed from human settlements were expected to safeguard the least impacted animal populations [45,46]. Therefore, we used the Euclidian distance between each CT station and the nearest PA boundary as a proxy of distance from human activity.

The uncontrolled grazing of domestic livestock within PAs is relatively common in tropical regions, potentially altering habitat structure and posing considerable threats to plant and animal populations [21,47]. Additionally, carnivores may be actively persecuted by humans to either prevent or retaliate livestock depredation [48,49]. Focal interviews at the surveyed reserves prior to this study revealed that surrounding human settlements typically raised free-ranging cattle that used reserve areas as grazing and browsing rangelands. Hence, we decided to use CTs to explicitly quantify cattle capture rates as an additional proxy of human pressure, here calculated as the sum of all independent cattle events. To use this variable as an occupancy covariate, for each CT station we divided the number of independent events by the total number of CT days sampled. Cattle detection rates were therefore included both as occupancy and detection covariates in different multivariate models.

Elevation at each camera-trap station, obtained from the digital elevation layer of the Shuttle Radar Topographic Mission (SRTM, <http://srtm.csi.cgiar.org/>), was used to assess one of the potential environmental gradients that could affect species occupancy. Additionally, the proportion of forest area within a 10-km radius from each camera-trap station, obtained from the GlobCover 2009 Land Cover Map (<due.esrin.esa.int/globcover/>), was also incorporated into occupancy and detection probability. All land cover categories representing different forest types were pooled together and used as a single category. Spatial analyses were implemented in ArcGis (v. 10.0) and Global Mapper (v. 9) software.

Understory structure may influence patterns of habitat use of medium- and large-sized mammals, thereby affecting species occupancy patterns [50,51]. We therefore obtained a measure of understory density at each CT station to represent the variation in understory structure. This was done by counting the number of visually unobstructed 10-cm divisions of a 1-m graduated pole placed vertically at 10 meters from the observer. A higher understory density was also expected to reduce the detection range of camera traps and was thus included as a detection covariate.

Data analysis

The use of occupancy models to analyze data obtained from camera-trapping methods has become increasingly popular due to its straightforward ability to account for imperfect detections of surveyed animals [52,53] by providing both occupancy (ψ) and detection (p) probability estimates for each sampling site. In this study, we modeled the occupancy probabilities for each species using the presence or absence of each study species (based on their CT detection rates) as a response variable, and considering every 5 consecutive day survey period as an independent repeated visit. Because each PA was surveyed for a period no longer than 65 days (SCNP = 65; RCES = 20; CSNF = 55), our models assumed that no changes in occupancy occurred during each survey period (single-season occupancy models). Although survey effort varied across all PAs, the occupancy models conducted provide a great flexibility allowing unequal sampling design [53,54]. Due to the large home ranges of most species examined here, especially carnivores, occupancy estimates were defined as the proportion of sites used by the species, assuming that individuals moved randomly both within and outside our sampling sites [53,55]. Finally, we assumed that all detections were correctly identified at the species level.

To assess differences among the three surveyed reserves, we included them as an additional categorical variable in the occupancy models, and considered each reserve as distinct levels of analysis. The inclusion of these PAs as an additional variable in the global models also had the advantage of accounting for the coarse spatial structure found in this extensive study area.

All explanatory variables were standardized before occupancy rates were modelled. For each species we used a multimodel inference approach, which provided the most parsimonious models from all possible first-order candidate subsets of the global models, here defined as the set of models with $\Delta AIC_c \leq 2$. For model sets with no single best models — here defined as models with Akaike weights ≥ 0.90 resulting in sets with similar competing candidate models in their data fit — a model-averaging approach was conducted to both account for model selection uncertainty and obtain a single predictive model for each species with model-averaged coefficients [56]. Occupancy models and model-averaged coefficients were computed using R version 3.0.2 [57] with the unmarked [54] and MuMIn [58] packages.

Results

Overall, a total survey effort of 2,710 camera-trap days was allocated to the three reserves with a mean of 36.6 ± 25.3 SD camera-trap days per station, resulting in a total of 468 independent records of the six selected species (S1 Table). Records from 13 additional medium- and large-bodied native mammal species were also obtained during our surveys (S1 Table), including the following five carnivore species: little spotted cat (*Leopardus tigrinus*), jaguarundi (*Puma yagouaroundi*), striped hog-nosed skunk (*Conepatus semistriatus*), tayra (*Eira barbara*), and crab-eating raccoon (*Procyon cancrivorus*). Photographs of domestic cattle (*Bos indicus*) were only obtained within RCES, but we also confirmed cattle presence inside the other two reserves during the study period. Additionally, surveys confirmed the occurrence of free-ranging feral dogs (*Canis familiaris*) within all three reserves (S1 Table).

Species occupancy

All variables included in the global models varied consistently in their relative importance in explaining the variation in occupancy probabilities across the different species, with Akaike weights, based on the sets of most parsimonious models, ranging from 0 to 1, and the summing weight (Σw) across species ranging from 5.0 to 0.76 (Table 1).

With the exception of black-rumped agoutis, patterns of occupancy of all study species were significantly different across the three reserves, with reserve denomination being retained in all top-ranked models (wAICc=1; Table 1). With the exception of black-rumped agouti, results also indicate that SCNP is the reserve with the highest occupancy probabilities for all species (Table 2).

Table 1. Cumulative Akaike weights ($wAIC_c$) for environmental and anthropogenic variables for the set of top-ranked models ($\Delta AIC_c \leq 2$) obtained for each species examined here. Model parameters include Protected Area (PA), distance to the PA edge, proportion of forest area, frequency of cattle, elevation, and understorey density (UD).

Parameter	Type	Covariate	*jaguar*	*puma*	*Ocelot*	*crab-eating fox*	*gray-brocket deer*	*black-rumped agouti*	*Σw covariate*	*Σw type*
Ψ	Env	PA	1	1	1	1	1	-	5	9.49
		Elevation	0.84	0.13	0.16	0.62	-	0.06	1.81	
		forest cover	0.14	0.94	-	-	0.78	0.06	1.92	
		UD	0.11	-	-	0.22	-	0.43	0.76	
	Anthro	Edge distance	0.16	0.13	1	0.06	1	-	2.35	4.36
		Cattle	-	0.61	0.68	0.06	-	0.66	2.01	
P	Env	UD	0.13	0.31	1	0.22	1	0.77	3.43	3.43
	Anthro	Cattle	-	0.22	0.16	0.25	0.74	0.48	1.85	1.85

Table 2. Model-averaged parameter estimates and their unconditional standard errors (in parentheses) from top-ranked models ($\Delta AIC_c \leq 2$) obtained for each species. ^{a}difference between the mean value of CSNF and ESRC; ^{b}difference between the mean value of SCNP and ESRC

Parameter	Type	Covariate	*jaguar*	*puma*	*ocelot*	*crab-eating fox*	*gray-brocket deer*	*black-rumped agouti*
Ψ	Env	Intercept	-9.92 (223.02)	-8.67 (45.35)	-7.65 (21.59)	-0.01 (1.1)	-2.88 (2.18)	-0.31 (1.49)
		PA^{a}	-5.87 (873.58)^{a} 10.71 (223.02)^{b}	2.05 (4.07)^{a} 6.80 (4.02)^{b}	2.71 (2.52)^{a} 5.32 (2.02)^{b}	-11.46 (101.31)^{a} 0.41 (1.1)^{b}	1.57 (3.06)^{a} 4.29 (2.84)^{b}	-
		Elevation	-6.31 (4.59)	-6.71 (4.9)	-3.56 (4.29)	-3.91 (2.62)	-	1.39 (1.53)
		forest cover	2.04 (2.43)	-4.39 (1.91)	-	-	-3.16 (1.65)	0.52 (0.78)
		UD	-0.21 (0.92)	-	-	-0.72 (0.67)	-	0.99 (2.63)
	Anthro	Edge distance	1.20 (1.52)	0.70 (0.87)	2.07 (1)	-0.35 (0.51)	2.04 (1.16)	-
		cattle	-	-5.96 (1.74)	-5.61 (25.95)	-0.08 (0.16)	-	0.85 (0.58)
P		Intercept	-1.51 (0.19)	-1.50 (0.27)	-0.76 (0.13)	-1.29 (0.2)	-1.26 (0.18)	-2.53 (0.55)
	Env	UD	-0.21 (0.25)	0.41 (0.3)	-0.62 (0.17)	-0.24 (0.23)	0.55 (0.21)	-1.53 (0.72)
	Anthro	cattle	-	1.95 (1.74)	1 (1.17)	-0.52 (0.62)	0.39 (0.21)	-0.64 (0.64)

Beyond reserve identity, the two variables representing anthropogenic activities, namely distance to park boundaries and frequency of cattle records, were the covariates with the greatest influence on overall species occupancy, with summed Akaike weight values of 2.35 and 2.01, respectively (Table 1).The majority of species tended to exhibit higher occupancies in core areas farther from park boundaries, with the exception of crab-eating fox, which were more common near boundaries, and black-rumped agouti which did not include this variable in any of its top ranked models (Table 1; Fig. 2). Ocelot and gray-brocket deer occupancies were heavily influenced by distance to park boundaries (estimates ± SE overlapped 0), whereas jaguar, puma and crab-eating fox were only weakly affected by this variable (Table 2).

Puma, ocelot and crab-eating fox occupancies responded negatively to the frequency of bovine cattle records, whereas black-rumped agouti occupancy was positively related to cattle (Table 2; Fig. 2). The effect of this variable was more evident for puma and black-rumped agouti occupancies but weak for crab-eating fox and ocelot.

Fig. 2. Model-averaged predicted curves of species occupancy probability (ψ) in response to each of the standardized covariates included in the models, with all other covariates held constant.

Other environmental variables were also important in explaining part of the variation in occupancy across species, with elevation having a negative effect on the occupancy probability of most study species, except for black-rumped agouti which presented a lower occupancy probability in lowland areas, and gray-brocket deer which did not include elevation in its top ranked occupancy models (Table 2, Fig. 2). The effect of this variable was strong for jaguar, puma and crab-eating fox occupancies but weak for ocelot and black-rumped agouti (Table 1). An increase in the proportion of dry forest cover was the variable with the highest variation across species, strongly affecting puma and gray-brocket deer, weakly affecting jaguar and black-rumped agouti occupancies, and having no effect on ocelot and crab-eating fox. Puma and gray-brocket deer favored more open-habitat areas with a lower proportion of forest, whereas jaguar and black-rumped agouti responded positively to forest cover (Table 2; Fig. 2). Finally, jaguar and crab-eating fox were less prevalent in areas characterized by a sparse understorey, whereas understorey density had a positive effect on agouti, but was not included in any of the top ranked models for puma, ocelot and gray-brocket deer (Table 1 and 2; Fig. 2).

Species detectability

Understory density was relatively important in explaining the variation in species detection across all species, with jaguar, ocelot, crab-eating fox and black-rumped agouti exhibiting negative responses to understory density, whereas puma and gray-brocket deer responded positively to an increase in the same variable (Table 2; Fig. 1). This variable had a strong effect on the detection probabilities of ocelot, gray-brocket deer and black-rumped agouti, and a weak effect on the remaining species (Table 2). The frequency of cattle records had a weak influence on the detectability of all species, with puma, ocelot and gray-brocket deer detection probabilities responding positively to an increase in cattle frequency, whereas crab-eating fox and black-rumped agouti responded negatively to the same variable (Table 1, 2; Fig. 1).

Discussion

This is to our knowledge the first study to systematically evaluate large mammal occupancy responses to habitat structure and anthropogenic disturbance within protected areas of the Brazilian Caatinga. The high heterogeneity of the Caatinga biome, with a conspicuous diversity of structurally distinct vegetation types, combined with the wide range of physical characteristics found in the study area, are expected to affect patterns of species distribution in this biome. The fact that the fine-scale occurrence of all species were strongly influenced by at least one of the three environmental variables examined here corroborates the importance of using such predictors as proxies of key environmental gradients affecting the local ecological distribution of terrestrial mammals [e.g. 52,60,61].

A study on the potential ecological distribution of jaguar in both protected and unprotected areas of the Caatinga biome, showed a positive relationship between elevation and jaguar habitat suitability [62]. This is, however, contradicted by our results which yielded an inverse relationship, suggesting that jaguars favored low-elevation areas. The apparent discrepancy between these studies is likely explained by the negative correlation between elevation and the intensity of human occupation, thereby obscuring the effectively *higher* suitability of low-elevation habitats to jaguars. The fact that our study was entirely restricted to protected areas suggests that our results reflect the expected baseline occupancy patterns of jaguars where overall human disturbance is low, even in lowland areas. This deceptive pattern of habitat selection fits a wide range of so-called upland bird and mammal species worldwide whose former population densities and distribution were in fact much greater in previously undisturbed lowland habitats prior to expansion of human agriculture and livestock husbandry in their prime habitats [63].

Jaguars and pumas are known to occur sympatrically throughout a large part of their geographic ranges [64,65]. However, different studies have shown that these two large cats tend to exhibit mutual avoidance and interspecific segregation by diverging behaviorally in many respects, including dietary composition and time of activity [66,67]. The fact that jaguars exhibited a consistently higher occupancy in more forested areas, whereas pumas had a strong tendency to occupy more open areas, supports the notion of a niche partitioning between these species expressed in terms of selection of available habitat types found within the Caatinga mosaic.

Effects of cattle on Caatinga mammal assemblages

Our results show significant between-species differences in local occupancy related to an intensification of pastoralist activities, likely evidencing the direct or indirect impacts of cattle on large mammals of the Caatinga. These effects could be more clearly detected on carnivore species, with three of the four carnivores examined here responding negatively to an increase in cattle records. Jaguar was the only carnivore species for which this variable was not included in the best supported models. This, however, can be explained by the absence of cattle records at SCNP, the only reserve in which jaguar CT records were obtained, thereby precluding a proper assessment of jaguar-cattle coexistence.

Crab-eating foxes are known to be generalist canids in their eclectic dietary habits, and less sensitive to anthropogenic disturbances, being frequently found in highly degraded habitats [68]. This is consistent with our results showing that this species was at least tolerant of cattle presence. Moreover, the fact that crab-eating foxes were more prevalent near park boundaries corroborates the idea that this species tends to behave as a human commensal, is highly resilient to human-modified landscapes, and is likely attracted to sites with a higher availability of food resources such as human waste and small livestock (e.g. poultry).

Unlike the patterns obtained for most carnivore species, both agouti and brocket deer were apparently not detrimentally affected where cattle were most frequent. Species with high population growth rates are, in general, less vulnerable to the impacts of hunting and other anthropogenic influences [69], particularly large caviomorph rodents [70]. Our study supports this tenet, with black-rumped agoutis responding positively to cattle incidence, showing higher abundance at shorter distances from reserve boundaries. It is reasonable to expect that predator population declines and/or low rates of habitat use in areas that are heavily used by cattle, as shown here, may also favor prey species like agoutis. Moreover, ambush predators frequently rely on dense understory structure to stalk prey [71,72], so we expect that changes in the vegetation structure from denser shrubland to a more open understory vegetation type due to a “browse line” typical of cattle overgrazing, may also have favored agouti habitat use.

Unexpectedly, occupancy of gray-brocket deer was not influenced by the presence of cattle. It is possible that potential antagonist effects related to pastoralist activities on this species may hinder the detection of the expected direct and indirect negative impacts, such as foraging competition between deer and cattle and hunting pressure. The decline in large carnivore occupancy in areas heavily used by cattle, and the resulting decrease in deer predation rates by these species may be an indirect positive effect counterbalancing any potential detrimental effects of cattle on wild ungulate populations.

Domestic and wild mammals are severely constrained by the availability of forage and water in semi-arid environments, and therefore exhibit seasonal movement patterns in order to maximize use of available resources in more mesic habitats. The fact that our study was restricted to a single dry season exposes a potential oversimplification of the interaction between domestic and wild mammals and their environment. However, because the dry season is the ‘lean’ period of most severe limitation of critical resources for both domestic and wild mammals, we expect this to be the period when any competitive interactions become most intensified, likely aggravating the effects of cattle on wildlife.

Free-ranging large-bodied domestic ungulates are expected to move over larger home ranges than smaller livestock species, potentially leading to higher rates of intrusion from nearby ranches to adjacent natural areas [72], which in this study were largely unfenced. Our findings corroborate this assumption, as we failed to detect any of the smaller domestic herbivores inside any of the surveyed protected areas, even though these species were widespread and common in nearby settlements. Moreover, because large livestock are less likely to succumb to attacks inflicted by large felids in the Caatinga, because they were intrinsically rare in these landscapes, ranch managers were also more vigilant with smaller livestock, including goats and sheep, restricting their herd movements more rigorously than those of cattle.

Conservation effectiveness of protected areas

Apart from the aforementioned variables, a number of other factors are likely to operate synergistically in limiting the abundance and distribution of large mammal species, affecting mammal assemblages across the surveyed PAs. Although some of these influences are unlikely to be of anthropogenic origin, it is possible that these assemblages are further affected by the limited capability of these reserves to mitigate the multiple impacts of local human populations. One such factor that may considerably impair the persistence of terrestrial mammal populations, for example, is reserve size. Morato et al. [73], for example, estimated a minimum continuous Caatinga area of 1,700 km^2 to sustain a viable jaguar population, and a single individual jaguar may require a home range of up to 260 km^2, given the prey productivity of Caatinga habitat [74]. This highlights the need of future systematic planning when designing PAs to sustain wide-ranging carnivore populations, particularly large cats which have the largest spatial requirements of the species examined here. Moreover, all survey sites were embedded within a highly fragmented landscape, leaving these reserves as one of the last few relict areas where large mammal populations sensitive to habitat loss and chronic human pressure are likely to persist. The small size of CSNF, which is eight and nine times smaller than SCNP and RCES, respectively, clearly illustrates a poorly designed reserve providing insufficient amounts of habitat for many wide-ranging populations, which may partly explain the consistently lower occupancy values observed for most study species (Table 1, S2 Table). Moreover, spatial requirements to sustain any viable large mammal population in a semiarid environment will likely increase in the future as prolonged droughts in Northeast Brazil are becoming both more frequent and more severe under contemporary scenarios of climate change [75].

Even in well managed PAs, we can reasonably expect recently created reserves to be at their initial stages of faunal recovery, especially in areas with an intense history of natural resource overexploitation on low-fecundity species, such as large mammals and particularly carnivores [70]. Again, the fact that CSNF was only established in 1999, whereas SCNP and RCES were created in 1984 and 1979, respectively, seems to support this notion.

A third aspect likely to affect such areas is the level of natural resource use restriction imposed by each protected area category. Extractive practices are legally permitted in National Forests, which may incur additional negative direct or indirect effects on local mammal populations, thereby resulting in lower occupancy of species sensitive to these activities [76]. With a recent history of intensive timber extraction for coal production, CSNF was created as a National Forest with the intent of maintaining these extractive activities, so that any detrimental effects of habitat degradation on native mammal populations are unlikely to be reversed in the near future.

Although both reserve design and denomination criteria potentially affect the conservation performance of PAs, establishing sufficiently large PAs may not be enough to protect large mammal populations, even if they are strictly-protected on paper, if use restrictions are not properly enforced to inhibit the detrimental impacts of human intrusion and overexploitation [77]. Cattle herds were pervasive within the boundaries of RCES, which entirely violates the regulations of an Ecological Station, the PA category in Brazil that is one of the most restrictive on paper. This is further evidence of the lack of effective law enforcement to restrain illegal activities that directly contravene the objectives of this PA category. SCNP, on the other hand, is arguably the best managed PA throughout the entire Caatinga biome [4]. A large number of visitors to this national park is attracted to its pre-Columbian archaeological sites, which justifies a more effective management structure and significant additional financial resources from the federal government and a local NGO. This has enabled a larger contingent of park staff including the continuous presence of park guards, more intensive law enforcement, and a strong support from social and education programs that alleviate local dependence of neighboring settlements on natural resources inside the park [4]. This enhanced management structure was therefore reflected in both higher occupancies of most mammal species and consistently lower presence of cattle.

Despite the intrusion of domestic livestock into the PAs we surveyed, the fact that most species exhibited higher occupancies within core reserve areas suggests that these sites at least partly serve as important refugia for the conservation of local biodiversity, by minimizing potential human-mediated edge effects, including hunting, deforestation, firewood collection, and cattle overgrazing.

Conservation implications for terrestrial mammals across the Caatinga

Our results re-emphasizes the huge conservation importance of all reserves surveyed for the native mammal fauna of the Caatinga, confirming the presence of large felids in all three reserves and the occurrence of other endangered mammal species, such as oncilla and Brazilian three-banded armadillo [34, S1 Table] in least one of the sites. Yet our results also corroborate the increasingly accepted idea that the contemporary Caatinga ecosystem and biodiversity has become gradually impoverished because of a long history of anthropogenic habitat modification and overhunting. For example, we were unable to find any evidence of some of the most harvest-sensitive mammal species in this biome, including white-lipped peccaries, giant anteaters, and tapirs, even though we surveyed three of the best remaining protected areas in the Caatinga. This was also the case of a neighboring region of the Atlantic Forest of northeastern Brazil, where these species had been driven to extinction at a regional scale [78]. These species have now either been extirpated at regional scales or occur at consistently low abundances in most of their Caatinga geographic range [79-83]. The fact that we failed to record some species expected to occur at our survey sites — yet our study included two of the largest, most faunally intact, and most important Caatinga protected areas — underscores the susceptibility of this biome to both historical and current threats. This also suggests that the status of these large mammal species is far worse in other protected areas and obviously the vast countryside matrix of unprotected areas where all large wild mammals have long been extirpated.

Jaguar populations persisting within the Caatinga biome are known to be highly fragmented and to be restricted to only a few areas, with SCNP being a key conservation area for the species [62, 84, 85]. The high rate of jaguar photographic captures, together with the species occupancy probabilities obtained for SCNP supports previous studies, which estimated a high density of jaguars within the reserve area [86-88]. These results and the fact that no jaguar record was obtained at the two other protected areas surveyed here confirm the paramount importance of SCNP as one of the last jaguar strongholds within the Caatinga biome.

Domestic herbivores in private lands adjacent to Brazilian semi-arid protected areas often rely on free-for-all resources found within these natural areas to subsist, especially during long dry seasons when the scarcity of forage and water becomes most severe. Poorly managed and weakly enforced protected areas are more prone to suffer from external threats, and reserves devoid of effective law enforcement measures may become “tragedy of the commons” rangelands shaped by communal pastoralists, eventually leading to the overexploitation of local natural resources, and the ensuing degradation of natural environments together with the decline or extinction of wildlife populations [89]. Such local dependence on natural capital provided by adjacent nature reserves should not be overlooked by PA managers, and be managed so that this coexistence does not result in severe impacts on native plant and animal populations and does not compromise the livelihoods of local human populations.

Human-wildlife conflicts are more prone to occur in areas where domestic and wild mammals coexist, due to livestock depredation by natural predators, leading to their persecution by cattle managers and bounty hunters [90]. Even when domestic animals do not use areas confined within PA boundaries, the inverse may frequently happen, with large felids frequently roaming outside these areas and, eventually, preying on domestic livestock. This problem was confirmed by previous interviews with reserve managers at SCNP and RCES and local informants conducted by the authors. Cattle restriction or reallocation to areas with lower natural predation probability or of lower conservation priority, for example, may be the best available measure that has proved to be an effective strategy in specific cases [91]. Voluntary resettlement of affected pastoralists to areas of lower conflict probability is another possible alternative to solve the problem of cattle intrusion into protected areas. Though human resettlements may be perceived as a drastic measure, in some cases it may be the only reasonable alternative that actually receives resounding support from local communities, as livestock managers are also interested in potential solutions that prevent or compensate their financial losses [92]. Finally, a number of different non-lethal methods aimed to mitigate carnivore depredation has been successfully applied to minimize livestock losses and associated human retaliations against these species [90], and could be used as a way to mitigate potential conflicts. Aversive or disruptive techniques, such as the use of domestic dogs, or visual (e.g. artificial light) and auditory stimulant devices (e.g. firework, speakers) that are able to condition the behavior of natural predators to a less conflictive pattern, are examples of desirable strategies likely to produce positive results [93,94].

Although sheep and goats were not found in any of the surveyed PAs, they are the two most important and numerically abundant livestock species currently raised throughout the Caatinga rangelands, after bovine cattle (S1 Fig). Cattle, sheep and goats are expected to affect the environment differently, due to their divergent dietary composition and foraging habits, among other factors [95]. Hence, further studies which include an assessment of the potential impacts of goats and sheep on the region are needed to maximize the habitat integrity of remaining areas of the Caatinga biome. It is reasonable to expect, in the long term, a gradual turnover in the species composition of Caatinga livestock, due to the ongoing wooded habitat loss and the potential effects of climate change, resulting in a higher prevalence of more xeric-adapted smaller grazing livestock, such as goats [96].

Given the severe conversion and degradation of its environment due to a myriad of anthropogenic stressors, which include the clearing of natural areas for livestock, agriculture, coal production, firewood collection, overgrazing of Caatinga scrub, and wildlife harvesting, the Caatinga region is an important biome that has been hitherto neglected by most governmental and non-governmental environmental initiatives [4,5]. Our study highlights the importance of existing PAs in protecting wild mammal populations, and the need of measures to minimize the effects of local human populations on wildlife populations. Because human settlements within the Caatinga have been historically the poorest in Brazil [97] and currently suffer from one of the most severe droughts ever recorded [98], it is crucial, therefore, that any strategies to conserve wildlife populations take into account the thorny socio-economic challenges of the region, maximizing the probability of reconciling the interests of both natural ecosystems and human populations.

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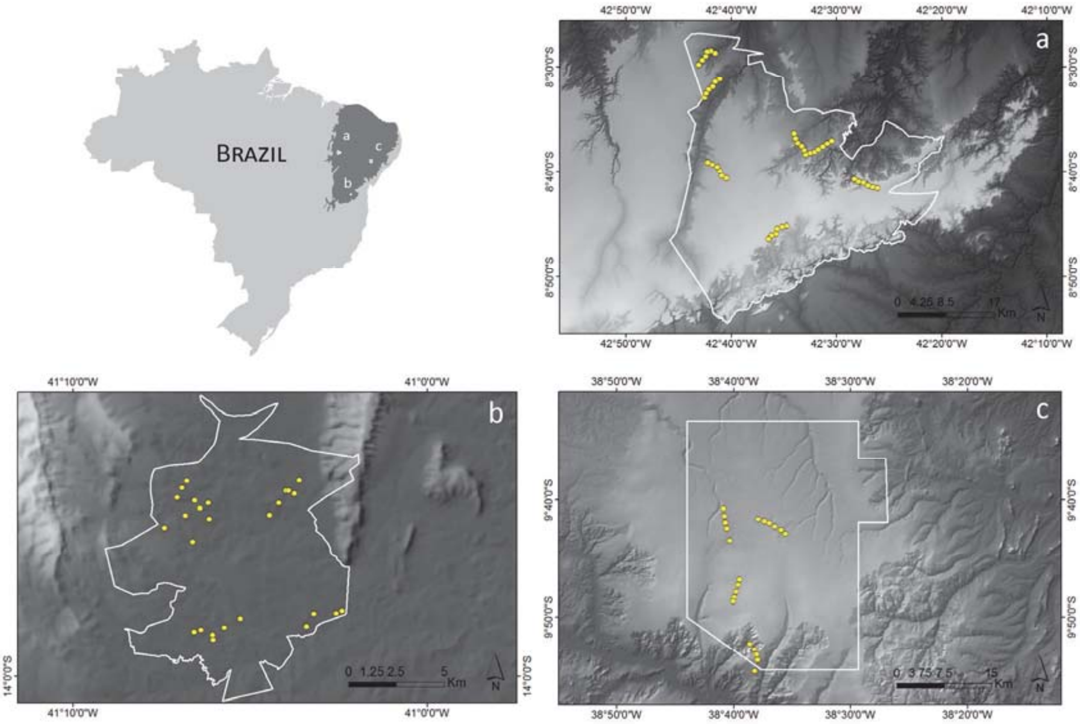


Fig. 1. Map of the study area showing the location of the three protected areas surveyed. a) Serra da Capivara National Park (SCNP), b) Contendas do Sincorá National Forest (CSNF), and c) Raso da Catarina Ecological Station (RCES). The map also depicts the 832,000-km^2 Caatinga biome within the drought polygon of northeast Brazil (shaded area). Yellow dots indicate camera trap survey sites within the three reserves.

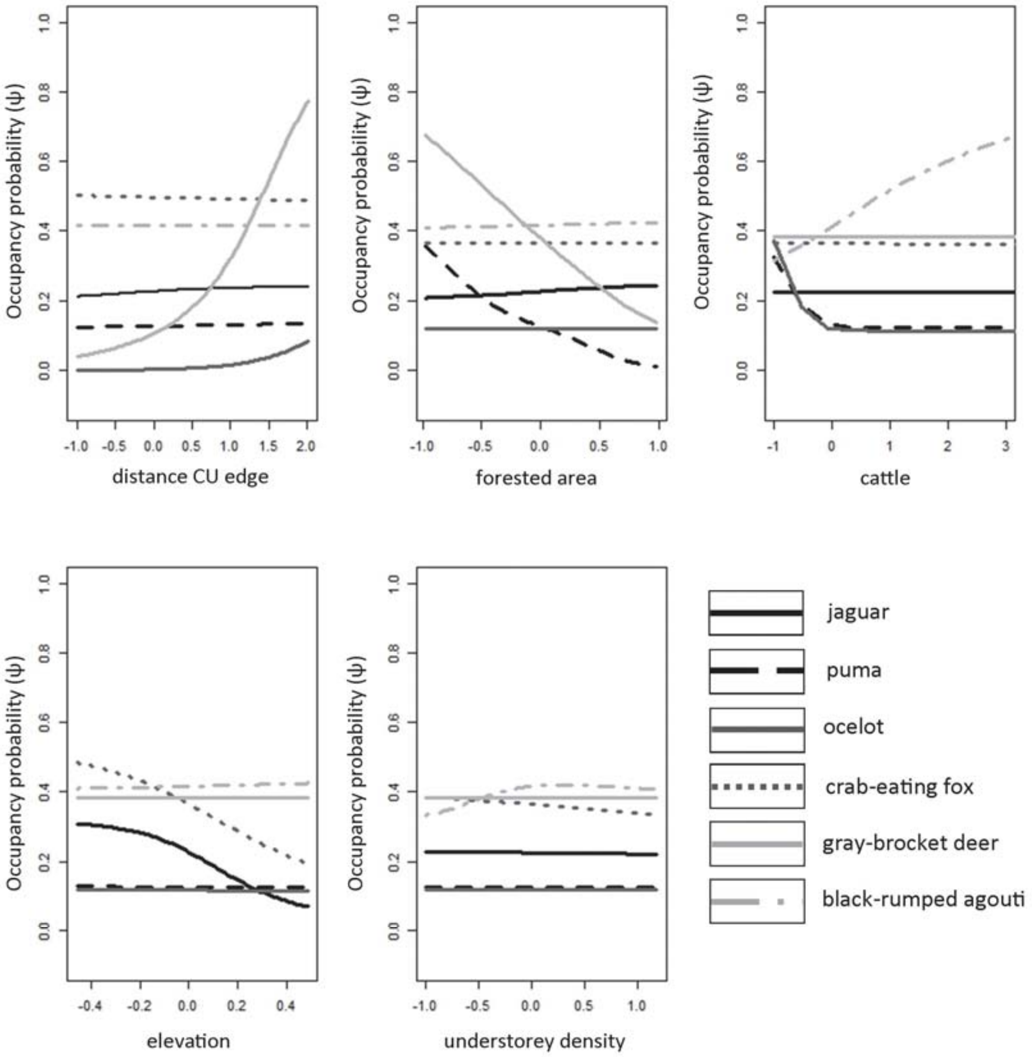
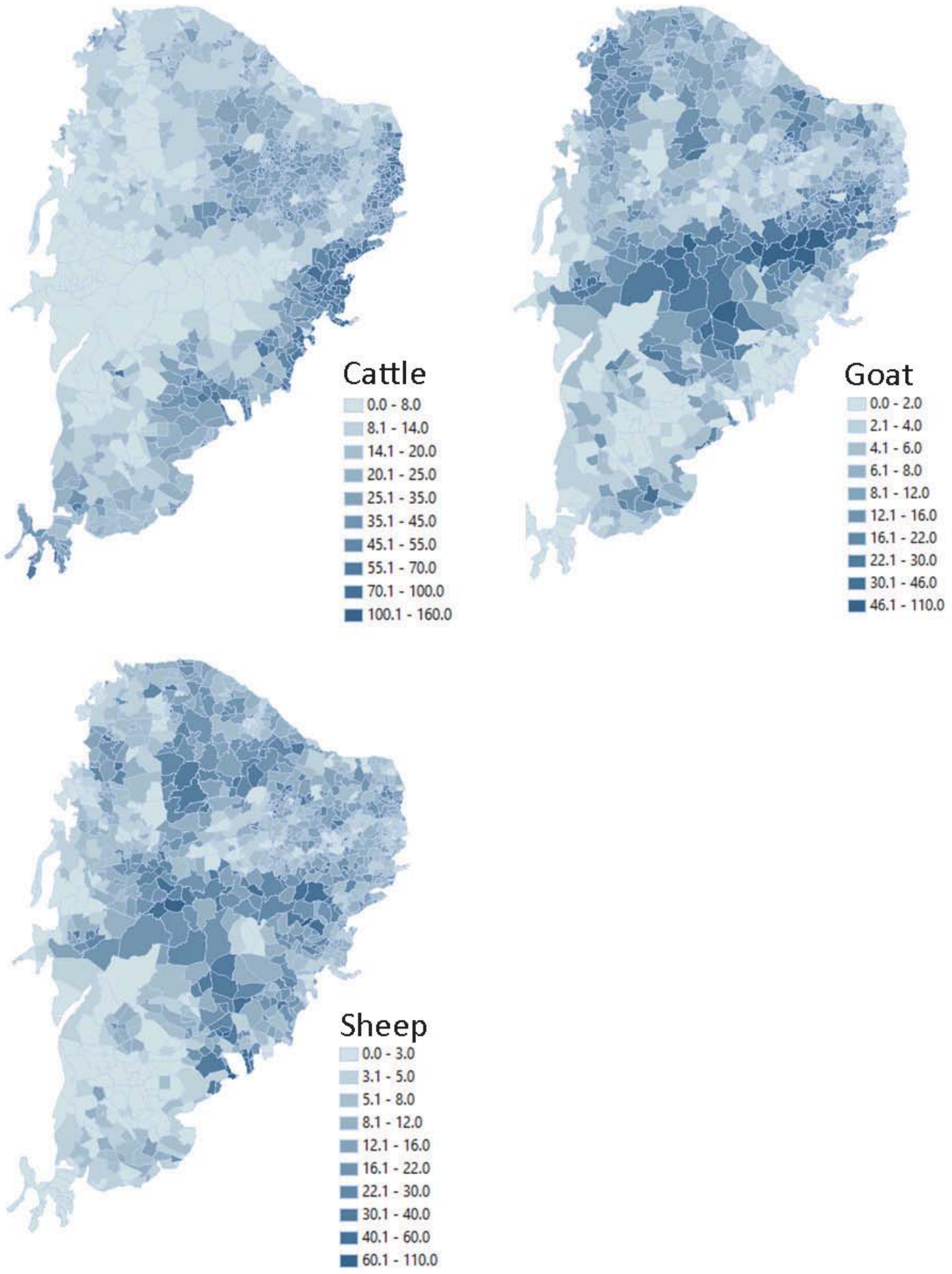


Fig. 2. Model-averaged predicted curves of species occupancy probability (ψ) in response to each of the standardized covariates included in the models, with all other covariates held constant.

Supporting Information

S1 Table. Summary of medium- and large-sized mammal species* recorded during this study and their respective capture rates. *Species nomenclature follows de Oliveira (2004). **number of independent records per camera trap-day shown in parentheses ***medium = 1-10 kg; large= >10 kg

Order	Family	Species	English names	Total records	Number of records**			diet	habit	body size***
					RCES	CSNF	SCNP			
Carnivora	Felidae	*Panthera onca*	jaguar	59	0	0	59 (0.138)	carnivore	terrestrial	large
		Puma concolor	puma	53	2 (0.005)	5 (0.004)	46 (0.022)	carnivore	terrestrial	large
		Leopardus pardalis	ocelot	143	1 (0.002)	3 (0.002)	139 (0.066)	carnivore	terrestrial	medium
		Leopardus tigrinus	oncilla	7	0	1 (0.001)	6 (0.003)	carnivore	terrestrial	medium
		Puma yagouaroundi	jaguarundi	6	0	0	6 (0.003)	carnivore	terrestrial	medium
	Canidae	*Cerdocyon thous*	crab-eating fox	70	4 (0.009)	0	66 (0.031)	omnivore	terrestrial	medium
		Canis lupus familiaris	domestic (feral) dog	5	1 (0.002)	3 (0.002)	1 (>0.001)	omnivore	terrestrial	medium
	Mustelidae	*Conepatus semistriatus*	striped hog-nosed skunk	8	0	2 (0.002)	6 (0.003)	omnivore	terrestrial	medium
		Eira barbara	tayra	5	5 (0.012)	0	0	omnivore	scansorial	medium
	Procyonidae	*Procyon cancrivorus*	crab-eating racoon	1	0	1 (0.001)	0	carnivore	terrestrial	medium
Primates	Cebidae	*Cebus apella*	black-capped capuchin	3	0	0	3	omnivore	arboreal	medium
Artiodactyla	Cervidae	*Mazama gouazoubira*	gray brocket deer	120	16 (0.037)	2 (0.002)	102 (0.048)	herbivore	terrestrial	large
	Tayassuidae	*Pecari tajacu*	collared peccary	8	2 (0.005)	0	6 (0.003)	omnivore	terrestrial	large
	Bovidae	*Bos indicus*	Zebu cattle	59	59 (0.138)	0	0	herbivore	terrestrial	large
Xenarthra	Dasypodidae	*Dasypus novemcinctus*	nine-banded armadillo	6	3 (0.007)	0	3 (0.001)	insectivore	fossorial	medium
		Tolypeutes tricinctus	Braz. three-banded armadillo	7	5 (0.012)	0	2 (0.001)	insectivore	fossorial	medium
	Myrmecophagidae	*Tamandua tetradactyla*	collared anteater	2	0	0	2 (0.001)	insectivore	scansorial	medium
Rodentia	Dasyproctidae	*Dasyprocta prymnolopha*	black-rumped agouti	23	10 (0.023)	2 (0.002)	11 (0.005)	herbivore	terrestrial	medium
	Erethizontidae	*Coendou prehensilis*	Brazilian porcupine	1	0	0	1 (>0.001)	herbivore	scansorial	medium



S1 Fig. Map of the Caatinga biome across all 10 states of northeastern Brazil showing the cattle, goat and sheep densities (head per km^2) at the municipal county level. Source: IBGE 2011.

S2 Fig. Camera-trap images of all six species examined in this study. a. jaguar (*Panthera onca*), b. puma (*Puma concolor*), c. ocelot (*Leopardus pardalis*), d. Crax-eating fox (*Cerdocyon thous*), e. black-rumped agouti (*Dasyprocta prymnolopha*), f. gray brocket deer (*Mazama gouazoubyra*).

PAPER IV

Paper IV aims to better understand the current status of an important, albeit poorly studied, Near Threatened game species - the Orinoco Goose. This was done by assessing the species occupancy patterns within the study area, related to both environmental and human variables. The impacts of human populations on the species was also assessed by monitoring the species offtake by local hunters.

Photo: W. Endo

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Seasonal abundance and breeding habitat occupancy of the Orinoco Goose (*Neochen jubata)* in western Brazilian Amazonia

WHALDENER ENDO, TORBJØRN HAUGAASEN and CARLOS A. PERES

Summary

The Near-threatened Orinoco Goose *Neochen jubata* is a poorly known South American sheldgoose with a declining population and range distribution. In this study, we surveyed the Orinoco Goose population along the middle reaches of the Rio Juruá, western Brazilian Amazonia, and its first-order tributaries. We quantified the seasonal abundance of geese, pinpointed their approximate breeding season, and examined their habitat associations and the potential effects of human activities on their abundance. Hunting by local villagers was also monitored to assess the offtake rate of this species. Orinoco Goose occurrence in the region was highly seasonal and restricted to the dry season. We estimated a mean dry-season encounter rate of 7.18 ± 2.45 adult individuals per 4-km section along this river. Immature individuals were seen along the river margins from August to December. The species showed a strong preference for sandy beaches and was primarily restricted to the main river channel, with few individuals occurring along tributaries. The encounter rate of this species was also significantly related to fluvial distance from the municipal urban centre and to the level of protection from hunting. Hunting of Orinoco Goose was reported in 12 of the 26 villages monitored. The seasonal appearance of the Orinoco Goose in the region indicates that this is a migratory population. Our study indicates that strict protection of the river margins, and sandy beaches in particular, along the main river channel is likely to be positive for the conservation of this species along the Rio Juruá. However, further knowledge of migration routes is critical for effective protection of both breeding and non-breeding populations.

Resumo

O quase-ameaçado pato-corredor *Neochen jubata* é um anatídeo sul-americano pouco conhecido e com uma população decrescente devido, principalmente, à intensa pressão de caça. Neste estudo, nós realizamos censos populacionais de patos-corredores ao longo do médio curso do rio Juruá, Amazônia Ocidental Brasileira, e de seus tributários de primeira ordem na região. Nós quantificamos a abundância sazonal de patos-corredores, definimos a época de reprodução e investigamos as associações de habitat e as potenciais influências de atividades humanas em sua abundância. Atividades de caça em comunidades locais foram também monitoradas a fim de avaliar a taxa de abate da espécie. A ocorrência da espécie na região foi acentuadamente sazonal e aparentemente restrita aos meses da estação seca. A taxa de encontro de indivíduos adultos durante essa estação foi estimada em 7.18 ± 2.45 ind/4 km de seção de rio. Indivíduos imaturos foram vistos ao longo das margens do rio e tributários durante o período de agosto-dezembro. A espécie demostrou uma forte preferência por praias arenosas e se mostrou basicamente restrita ao canal principal do rio Juruá, com poucos indivíduos encontrados ao longo dos tributários. A taxa de encontro da espécie foi também significativamente relacionada à distância fluvial do centro urbano municipal e ao nível de proteção de caça. A caça de patos-corredores foi registrada em 12 das 26 comunidades monitoradas. A ocorrência sazonal de pato-corredor na região sugere que essa é uma população migratória. Nosso estudo indica que regras de proteção restritas das margens do rio, e, em particular, das praias arenosas, podem ser benéficas para a conservação desta espécie na bacia do Juruá. No entanto, um melhor conhecimento das rotas migratórias é fundamental para uma proteção efetiva de populações reprodutivas e não reprodutivas.

Introduction

The Orinoco Goose *Neochen jubata*, a once common South American sheldgoose of the Anatidae family (Subfamily Tadorninae), is now a 'Near-threatened' species with a patchy distribution throughout its range (BirdLife International 2012). Although poorly assessed, the extant population is currently estimated at 10,000–25,000 individuals and believed to be declining (Delany and Scott 2006, BirdLife International 2012). The remaining strongholds for the species are a few sites in Venezuela (e.g. Esteros de Mantecal), Colombia (e.g. La Primavera), the Bení region of Bolivia and the Central Araguaia river region in Brazil (Hilty 2003, Kriese 2004, Pinheiro and Dornas 2009). The species occurs east of the Andes, with only a single report from west of the Andes to date (Aranzamendi *et al.* 2010). In the lowland Amazon Basin, where the Orinoco Goose is one of the most threatened bird species (Stotz *et al.* 1997, Whittaker 2004, Trolle and Walther 2004, Davenport *et al.* 2012), it is found at low densities along the Amazon and Orinoco rivers and tributaries. These populations are thought to be smaller and more fragmented than those in the Llanos region and in other open wetland habitats found in the Bení and the Araguaia river basins (Kriese 2004, Whittaker 2004, Brewer and Kriese 2005, Schulenberg *et al.* 2007).

Little is known about the natural history of the Orinoco Goose. The species is a terrestrial grazer, but seems to be invariably associated with areas providing immediate access to freshwater bodies, such as wet savannas and margins of large freshwater wetlands (Hilty 2003, BirdLife International 2012). The species is a secondary-cavity nester requiring large trees (DBH > 30 cm) with cavities for the species to breed successfully (Newton 1994, Kriese 2004).

Due to its large body size and preference for open habitats, the Orinoco Goose is a conspicuous target-species for hunters and hunting is currently suggested to be the most important driver of population declines (BirdLife International 2012). For this reason, effective measures to control the impacts of game harvesting in areas where it occurs are highly desirable.

The increasing number of large protected areas (hereafter, PAs) created over the last two decades within the Orinoco Goose's geographic range (ARPA 2010) is expected to potentially improve the conservation status of the species. Yet, most of these existing reserves consist of human-occupied PAs that support the livelihoods of either indigenous (Indigenous Territories) or non-indigenous populations (Extractive Reserves). These human populations are typically dependent on the local wildlife to supply their daily protein needs (Silvius *et al.* 2004). To overcome this issue, most existing PAs along major tributaries of the Amazon were created as sustainable-use PAs, where community-based management of extractive resources have few restrictions compared to strictly protected reserves (Peres and Zimmerman 2001).

In PAs that fall into the sustainable-use category, local human populations are expected to follow a set of management guidelines that attempt to combine extractive activities with the long-term persistence of exploited populations. Such measures may favour the creation of zoning systems, or areas under varying hunting restrictions, potentially providing critical wildlife refugia for exploited populations (Novaro *et al.* 2000). Despite the underlying assumption that multiple-use PAs can potentially prevent declines in hunted populations, the effectiveness of such PAs has been the subject of intense debate (Peres 2011). Here, we examine the conservation status and habitat occupancy of an Orinoco Goose population across a wide habitat mosaic under varying levels of subsistence hunting and extractive restrictions. We investigate spatio-temporal changes in the abundance of this species in relation to different levels of protection and other socioeconomic and environmental variables. We also provide information on the seasonal variation in the occurrence, habitat use, and reproduction of this species throughout our large study area.

Methods

Study Area

The study was conducted from March 2008 to August 2011 along the Rio Juruá, one of the main tributaries of the Rio Solimões (Amazon) located in western Brazilian Amazonia (Figure 1). The region is subjected to a well-defined seasonal rainfall regime, with a mean annual rainfall of 2,400–2,800 mm (Sombroek 2001). There is a strong seasonal oscillation in the river water discharge, with the period of low water level occurring from July to October (Figure 2). The region consists of both seasonally flooded forest (*várzea*) and areas of upland forest (*terra firme*). We selected a 392-km section of the Rio Juruá, ranging from the southernmost limit of the Carauari municipal boundary to the nearest point along the river from the municipal urban centre (Figure 1). The urban centre concentrates 77% of the entire municipal population of ~25,800 inhabitants, with the remaining population living in small rural villages spread mainly along the Rio Juruá and its major tributaries (IBGE 2010). The surveyed section of the river also intersects two sustainable-use forest reserves, the Médio-Juruá Extractive Reserve and the Uacari Sustainable Development Reserve (Figure 1). Both of these PAs have land-use zoning systems implemented within their areas. The most strictly protected sites in the region include nine sandy beaches along the main river, the purpose of which is to protect nesting sites for three freshwater turtle species (*Podocnemis* spp.) that are heavily persecuted by locals for their meat and eggs (Kemenes and Pezzuti 2007). In addition, four tributaries of the Rio Juruá were also surveyed (Figure 1): three tributaries located partially (Rio Eré) or fully (Rio Anaxiqui and Paraná do São Raimundo) within the Uacari Sustainable Development Reserve, and the Rio Xeruã, encompassed by two Indigenous Lands, the Deni Indigenous Territory and the Kanamari Indigenous Territory (Figure 1).

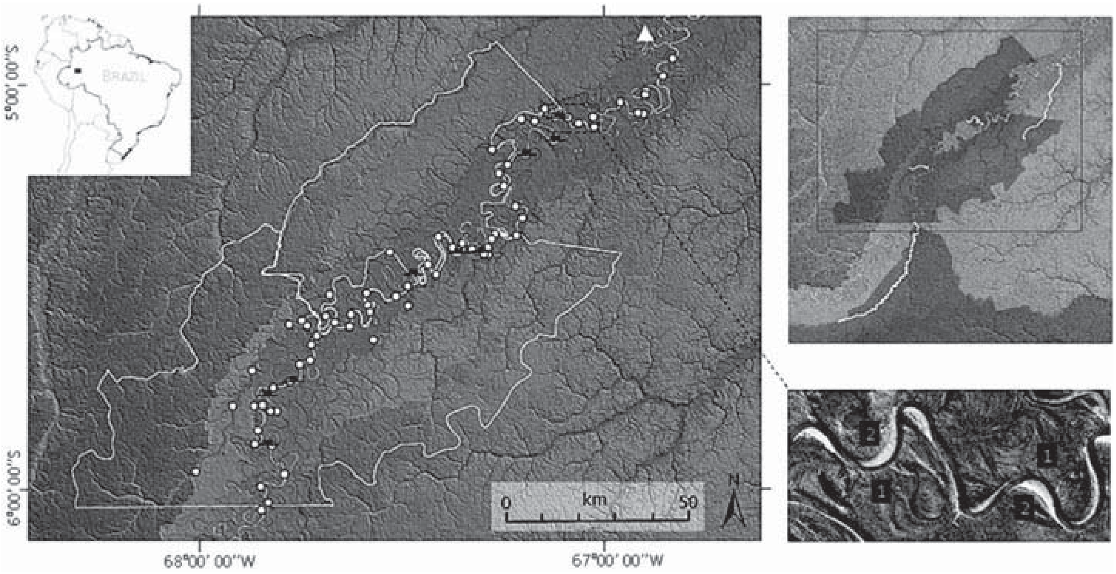

Figure 1. Map of the study area showing: the municipal urban centre of Carauari (white triangle), protected areas (white polygons), villages (gray circles) and protected *Podocnemis* turtle nesting sites (black icons); The inset map depicts the main tributaries of the rio Juruá surveyed (top right) and a small section of the surveyed area showing the river cut-bank (1) and sandy beach (2) sites formed along the meandering river (bottom right).

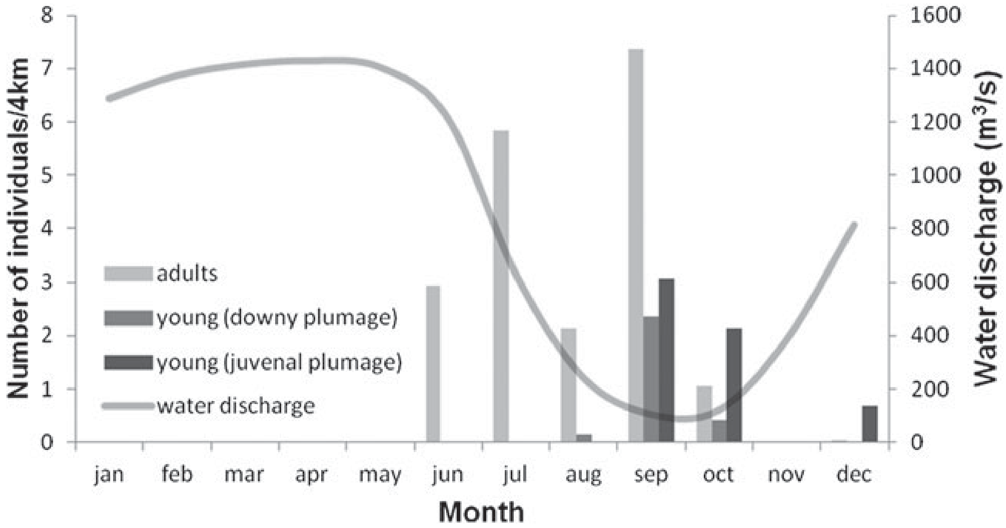

Figure 2. Monthly encounter rates of Orinoco Goose within the study area, and water discharge of the Rio Juruá measured at Porto Gavião for 2008-2010 (Source: Petrobras S.A).

Field Surveys

We surveyed Orinoco Geese by searching for and counting all individuals along both margins of the rivers. The surveys were conducted during all months of the year, except for November, using motorized boats with at least two observers carrying out the counts. The censuses were conducted between 06h30 and 18h30, but were discontinued whenever visibility was impaired by low light conditions or heavy rainfall. Individuals seen on the margins of the river or tributaries, flying, or on the water were recorded and their locations georeferenced. Observations were aided by a set of 10x42 binoculars. For large flocks or crèches of immature individuals, a digital SLR camera equipped with a 200 mm zoom lens was used to take reference photos, which were used as additional documentation to reliably count the total number of individuals, to discriminate adults from immature individuals, and to identify the plumage stage of each immature individual. All individuals close to each other (< 100 m) were counted as a single flock.

Adults were distinguished from immature individuals by their body size, plumage pattern and leg colour, with adults having more reddish legs than immature individuals. Brood size was assessed by counting the number of immature individuals clustered within a single flock and accompanied by at least one adult. We also separated goslings into two different age classes: 1) downy juveniles – recognized by their small body size and pale buff plumage, and 2) fledgling juveniles – individuals with their first flying plumage, similar to that of adults (Figure S1 in the online Supplementary Material).

The meandering nature of the river and the seasonal changes in water level create a strong process of erosion and sediment deposition along the river margins and the seasonally flooded riverbeds. Two broad but clearly distinct habitat categories can thus be observed along the river. Sandy beaches (Figure S1, top) are formed in areas with intense alluvial deposition, consisting of a marked gradient of early successional plant communities (Salo *et al.* 1986). The river cutbank, on the other hand, consists of areas with a recent history of erosion activity and is characterized by denuded clay soils and steeper slopes bordering late successional forests. To assess the preference of individuals for any of these two particular habitats we recorded the location of each individual encountered according to these habitat types. For all records we also noted whether the geese were found along the main river or its tributaries, and if found along tributaries, how far from the Rio Juruá they were.

Human effects on goose abundance

To assess the effect of human activities on goose abundance, we measured the fluvial distance along the river from the urban centre to the mid-point of each surveyed location (see Data Analysis). Additionally, we assessed the effects of nearby rural villages by measuring the distances along the river, stream or used path to every village found within a 5, 10 and 20-km radius from the mid-point of the same surveyed river section. Village size, defined in terms of number of inhabitants, was also used to evaluate the effects of local human population density on goose abundance. To examine if goose encounter rates were higher within areas under greater hunting restrictions, we compared the abundance of geese in areas subjected to three use restriction levels found across the study area: 1) sites outside any of the existing PAs and therefore potentially most exposed to hunting activities, 2) areas within any of these PAs and used exclusively by the villages found within their boundaries or adjacent areas, 3) strictly protected turtle nesting sites where all extractive activities were prohibited.

In addition, we also documented the number of Orinoco Geese killed by local people using weekly surveys deployed at 220 households belonging to 25 villages across the study area during the period of March 2008 to September 2010. All geese killed and consumed during this study period were recorded using a standardised questionnaire addressing all game species harvested at each household (see Newton *et al.* 2012, for a general description of these surveys).

Data Analyses

We evaluated differences in Orinoco Goose population abundance along the river by dividing the surveyed area into 98 sequential 4-km fluvial segments and considering each segment as a sampling unit. Although this procedure involves a certain degree of spatial correlation, this was explicitly accounted for in the analysis by including the linear distance from the urban centre as one of the covariates in the models.

For each fluvial segment, a human population density (HPD) index was calculated as a proxy for the aggregate effect of local village density and size on goose abundance. This index is based on both the size and distance of each village found within any given buffer area around each fluvial segment, and can be described as following:

$$HPD = \sum_{i=1}^{n} VS_i * (BR - VD_i)/BR$$

Where VS = village size (number of inhabitants), BR = buffer radius and VD = distance from the village.

To relate changes in species abundance to the explanatory variables we used generalized linear mixed models (GLMMs) with a Poisson error structure, appropriate for count data. Distance along the river to the urban centre, *HPD* and site protection status were considered as fixed variables. We also included as a covariate the total extent of beaches, which was measured within each fluvial segment using *Landsat* images. Finally, month and year were included in the models as nested random variables. These analyses were carried out using the *lme4* package for R (Bates and Maechler 2011).

To calculate the best possible models for the study we used a multi-model inference approach, comparing second-order Akaike Information Criterion (AIC_c) values, more appropriate for small sample sizes, for each possible candidate GLMM derived from the global model. We ranked the models by comparing each candidate model with the model with the lowest AIC_c, and considering models with $\Delta_{AICc} > 2$ as poor candidates (Burnham and Anderson 2002). Finally, we also calculated the Akaike weights, which provide an overall indication of model likelihood of being the best candidate compared to all other possible models (Burnham and Anderson 2002). The *MuMIn* package (Barton 2012) was used to run the analysis in R (R Core Team 2012).

Since the distance to the urban centre and protection status of fluvial segments were strongly correlated ($r_s = 0.768$; $P < 0.001$; Spearman's rank correlation coefficient) we conducted separate analyses by replacing each of these two variables and selecting the global model with lower AIC value using a multimodel inference framework. We also conducted the analysis using village effect variables with three different buffer radii (5, 10 and 20 km) and selecting the most parsimonious model.

Results

Population abundance

In total, 7,145 km of surveys were conducted along the Rio Juruá and its tributaries. Orinoco Geese were entirely absent between January and May, but frequently recorded between June and December. This corresponds to the months of low water level (Figure 2). The mean encounter rate of adults along the Rio Juruá was of 7.18 ± 2.45 ind./4 km (mean ± SD) in June–September, the months when they were most frequently encountered (Figure 2, Figure 3, Table 1). Encounter rates were considerably lower along the tributaries, where only 0.55 ± 0.34 ind./4 km were seen in June–October. Moreover, all individuals observed along the tributaries were located close to the confluence with the Rio Juruá (mean = 2.4 ± 1.7 km) with no record beyond 5 km from the margin of the river. Additionally, all these individuals were restricted to the portion of the tributaries embedded within seasonally flooded forest.

Most adults recorded were seen in pairs (n = 610; 52.8%) or small flocks up to six individuals (28.5%), with a mean flock size of 3.58 ± 4.17 (range = 1–37) individuals (Figure 4). Immature birds were encountered between July and December. Goslings were more frequently observed during months of lowest water level (Figure 2, Table 1), with an encounter rate of 2.02 ± 2.38 ind./4 km. While downy juveniles were found as early as August, fledgling juveniles were only seen from September to December. The mean brood size of downy juveniles was 7.19 ± 6.75 (n = 24; range = 2–35), while fledglings had a mean brood size of 8.2 ± 4.93 (n = 39; range = 1–24), but this difference was not significant (P = 0.16; Wilcoxon rank sum test).

Habitat use

Sandy beaches (Figure S1) were more intensively used as resting and foraging sites compared to river cut-banks; 94.1% of all 438 records were of individuals on sandy beaches, whereas only 6% involved individuals on river cut-banks.

The vast majority of individuals observed were either resting or foraging on the ground (n = 449; 94.4%), with only a few seen on the water (2.9%) or flying (2.7%). Most individuals observed on the water (n = 13; 85.6%) were immature individuals or adults with their brood. No individuals were seen perched in trees.

Hunting pressure

Orinoco Geese were killed and consumed in 11 of the 25 villages monitored. A total of 27 individuals were killed during the study period, resulting in a rate of 0.09 ± 0.13 individuals killed per household per year. Geese were killed exclusively by hunters living in villages along the margin of the main river. No geese were seen during the surveys in May, but four kills were recorded by hunters during this month.

Predictors of species abundance

A single model including all the explanatory variables used in the analysis was the best candidate model from the 16 possible combinations to explain the abundance of adult geese along the Rio Juruá (Table 2). The results show that the encounter rate is positively associated with the linear extent of sandy beaches, the availability of protected turtle nesting sites, and distance from the urban centre. Conversely, the encounter rates were negatively related to the HPD index. Finally, the HPD index with a BR constant of 5 km was the most significant candidate predictor among the three BR values.

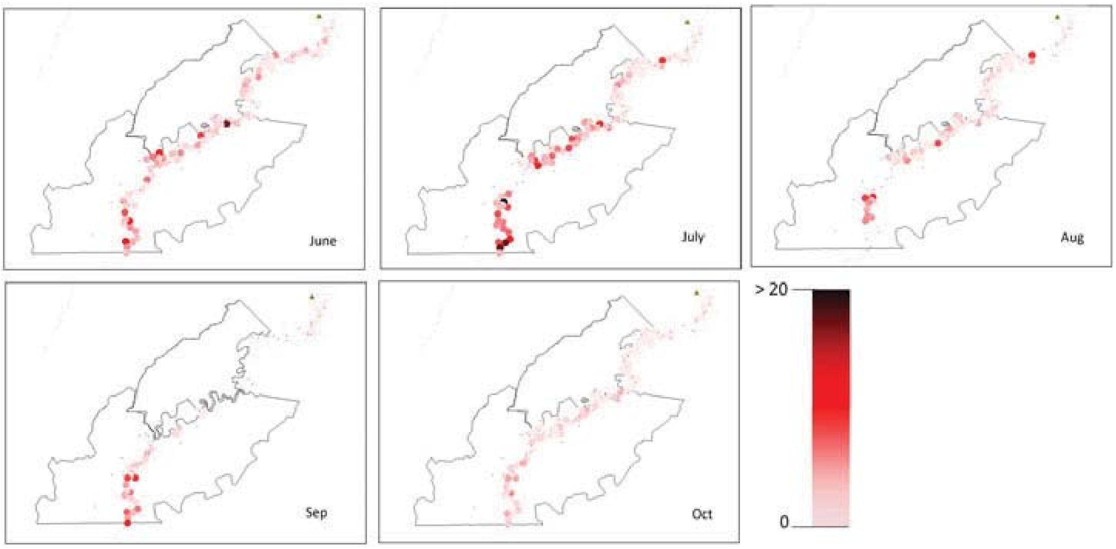

Figure 3. Encounter rate of Orinoco Goose along the middle rio Juruá between June and October. Colour coding is expressed as the total number of individual recorded per 4-km section of the river.

Discussion

We show that the Middle Juruá region of western Brazilian Amazonia is an important breeding area for several hundred Orinoco Geese, possibly supporting one of the largest populations known for the entire Amazon Basin to date. This region is therefore a key stronghold for the Orinoco Goose which has until now been largely overlooked. Sporadic visits to areas upriver of the surveyed section of the river suggest that goose abundance may be similar (W. Endo, pers. obs.), likely increasing the total number of individuals in the middle portion of the Rio Juruá to a few thousand individuals. Previous surveys in the upper portion of the Rio Juruá (Whittaker and Oren 1999) resulted in no records of geese and the absence of sightings during other surveys carried out in areas close to the junction of the Rio Juruá with the Rio Solimões (ICMBio 2009, R. Czaban *in litt.* 2013) may indicate that the species is restricted to the middle reaches of the Rio Juruá. Further studies are, nonetheless, required in the upper and lower portions of the Rio Juruá in order to properly estimate the Orinoco Goose population for this entire river basin.

The *várzea* floodplain forest is associated with a large number of oxbow lakes that remain partially unconnected to the Rio Juruá channel and its tributaries during the dry season. Observations of Orinoco Geese on the margins of lakes connected to the surveyed tributaries suggest that these lakes also serve as important foraging and brood rearing habitat for this species. Reports from local villagers also indicate that these lakes and lake margins are important nesting sites. The inclusion of such habitats in future surveys may therefore boost the population estimates for the region. The fact that a few geese were killed by hunters in May, when our surveys failed to record any individuals, support the notion that we are likely underestimating the total number of Orinoco Geese found in the study area.

The seasonal occurrence of Orinoco Geese in the study area suggests that this population migrates to other regions during the wet season. This migratory behaviour contrasts with most studies to date, which describe the species as non-migratory (del Hoyo *et al.* 1992, Stotz *et al.* 1997, Kriese 2004, Brewer and Kriese 2005). However, reports of a longitudinal migration of Orinoco Geese between southern Peru and northern Bolivia (Davenport *et al.* 2012) and the seasonal occurrence of another population in the Central Araguaia river region (De Luca *et al.* 2006) indicate that migratory behaviour is far more widespread than the Juruá population. The seasonal flood pulse which inundates important grazing sites may be one of the primary reasons for the evolution of such migratory behaviour among Orinoco Goose populations, and indeed other waterbirds (e.g. Black Skimmer *Rynchops niger* and

Table 1. Mean (± SD) monthly encounter rates of Orinoco Goose in the middle Juruá region, western Brazilian Amazonia.

	total		adult		downy juvenile		fledgling juvenile	
	mean	SD	mean	SD	mean	SD	mean	SD
Jan-May	0	0	0	0	0	0	0	0
Jun	2.93	4.35	2.93	4.35	0	0	0	0
Jul	5.84	10.87	5.84	10.87	0	0	0	0
Aug	2.27	4.29	2.14	3.93	0.14	1.15	0	0
Sep	12.79	18.04	7.36	9.57	2.36	5.28	3.07	6.98
Oct	3.6	6.9	1.06	1.72	0.42	1.62	2.13	5.02
Nov	-	-	-	-	-	-	-	-
Dec	0.7	2.92	0.03	0.17	0	0	0.67	2.87

Large-billed Tern *Phaetusa simplex*) dependent on riverine beach habitats that become flooded in the high-water season. Competition for suitable nesting sites has also been suggested as a potential factor leading birds to migrate to areas with a higher abundance of trees (Davenport *et al.* 2012). These observations, combined with the fact that all migratory populations are apparently restricted to the Amazon Basin, suggest that seasonal migration is the rule, rather than the exception, in this region.

The foraging constraints imposed by the seasonal flood pulse and river dynamics seem to be important determinants of habitat use in this species. The growing number of planned or approved hydroelectric projects within the species' geographic range is therefore likely to impact on the occurrence of this species in newly modified areas due to critical changes in inundation patterns (Tollefson 2011, Finer and Jenkins 2012).

The existence of large transient populations, such as that in our study area, suggests that populations previously considered to be independent are, in fact, the same populations that seasonally occupy different breeding areas. The occurrence of migratory populations may also pose a greater risk for the species (Davenport *et al.* 2012), potentially exposing these populations to a higher number of threats (Kirby *et al.* 2008). Further studies are clearly required to better understand the migratory behaviour of these transient populations in order to design an improved protection strategy for the species.

The fact that all individuals surveyed were distributed exclusively along sections of the river dissecting floodplain forests, coupled with the strong preference for sandy beach sites, make the Orinoco Goose a relatively selective bird in terms of habitat requirements. The Rio Juruá is one of the most meandering tributaries of the Amazon river (Latrubesse 2008). The high number of river bends with extensive sandy beaches may be one of the reasons facilitating the species' occurrence throughout

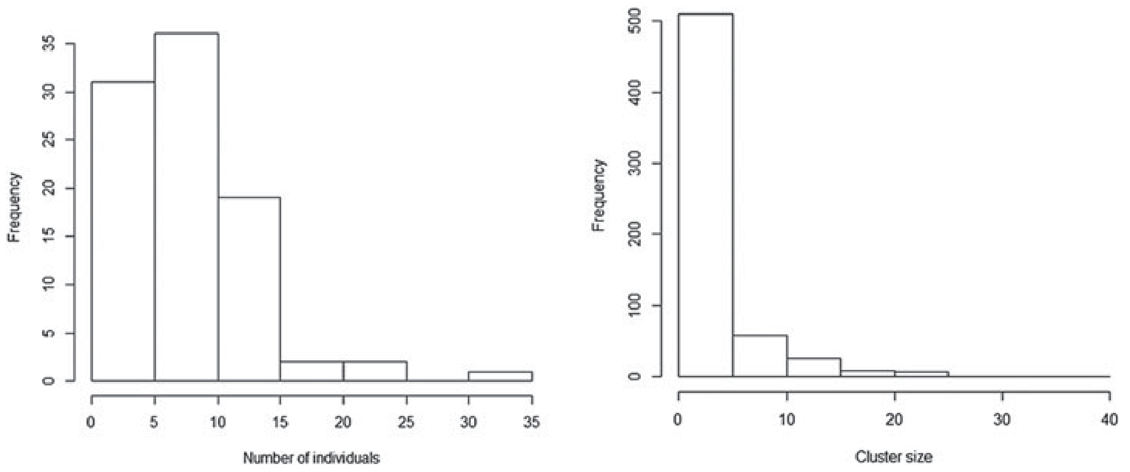

Figure 4. Brood size distribution of Orinoco Goose (mean = 8.59; SD = 5.25; left) and flock size (mean = 3.58; SD = 4.17 adults; right), in the middle Rio Juruá, western Brazilian Amazonia.

Table 2. Summary of generalized linear mixed model selection based on 16 candidate models predicting encounter rates of Orinoco Goose. Only the most parsimonious model ($\omega_i = 1$) and the two illustrative subsequent models are shown. LL = log-likelihood; K = number of parameters, AICc = Akaike's information criterion score corrected for small sample sizes; Δ_{AICc} = difference between a given model and the best model, in units of AICc; ω_i = Akaike weight for each model. Explanatory variables are coded as following, DST: distance from the municipal urban centre, BCH: proportion of sandy beaches within each fluvial segment, TRT: strictly-protected turtle nesting site, HPD: human population density.

Model rank	BCH	DST	TRT	HPD	LL	K	AICc	Δ_{AICc}	ω_i
1	0.2346	0.007482	*	-0.010820	-1240.633	5	2493.4	0	1
2	0.2475	0.007404		-0.011370	-1255.079	4	2520.3	26.84	0
3		0.007523	*	-0.008174	-1272.784	3	2555.7	62.25	0

the region. Our results also show that the Orinoco Goose mainly uses the main Rio Juruá channel as its preferred foraging and brood-rearing area, being conspicuously absent along most surveyed tributaries. This underlines the difficulty of providing satisfactory protection for the species. *Várzea* floodplain forests are, since pre-colonial times, some of the most intensively exploited Amazonian ecosystems (Roosevelt 1999). Margins of the main navigable rivers are also of high socio-economic importance for local semi-subsistence populations, being important areas for extractive and agricultural activities (Pinedo-Vasquez and Sears 2011, Newton *et al.* 2011). Consequently, any protection measures that impose constraints on local communities to exploit such areas are likely to meet local political resistance and be doomed to fail if not properly planned and implemented.

The brood size recorded here is consistent with the values of 6–10 goslings reported elsewhere (Brewer and Kriese 2005). Moreover, records of broods with considerably larger numbers of goslings confirm the common occurrence of intraspecific nest parasitism for the species (Kriese 2004) or the voluntary capture of immature individuals from other parents (Williams 1974). The stable values of brood size for goslings in different stages of development also indicate that the mortality rate is low during this life stage. The larger brood size recorded for older goslings, however, indicates that our surveys failed to obtain complete counts of downy fledglings. Additionally, the results showed a high proportion of fledgling juveniles compared to adults in December. This unbalanced proportion was partially due to observations of fully grown juveniles unassisted by their parents. However, this should be more carefully investigated in order to understand whether these individuals were in fact abandoned by their parents and able to migrate without parental guidance, or if we simply failed to detect the adults during surveys.

Orinoco Goose encounter rates increased significantly both in areas enjoying greater protection from hunting and areas farther from the urban centre of Carauari. The greater abundance of geese in areas under a higher level of protection suggests that these sustainable-development PAs have been effective in providing better protection for foraging and brood rearing.

The significantly higher encounter rate of geese in the surveyed segments including protected turtle nesting sites indicates that these sites may also benefit species other than freshwater turtles. Other vertebrate species known to use turtle nesting sites, such as wading birds (Caputo *et al.* 2005) and iguanas (Hirth 1963), could therefore benefit by such enforcement measures. However, effectively protected turtle nesting sites are small and sparsely distributed, and are therefore insufficient to fully protect the Orinoco Goose. The fate of the population will therefore continue to depend on the level of exploitation of surrounding areas, unless a larger number of beach nesting sites can be protected.

Despite records of Orinoco Geese being harvested by hunters in the study area, the low number of kills suggests that the species is hunted only opportunistically by local inhabitants. The number of geese killed represents a small fraction (1.1%) of the total number of game vertebrate kills recorded (n = 2,515) during the study period (W. Endo *et al.* unpubl. data). Yet, the continued exposure of this species to hunters converging on its preferred habitat renders this seasonal offtake an important issue shaping the future conservation status of the population. This mortality risk is further increased during the breeding season when adults display a more sedentary behaviour while rearing their brood along the margins of the river.

In summary, our results indicate that the Orinoco Goose is very habitat specific. While the preferred habitat is located in areas subjected to intense anthropogenic activities, our metric of abundance consistently showed that the geese were primarily restricted to the most sparsely settled and best protected areas. These findings, together with the transient behaviour displayed by the Juruá population, indicate that more refined and effective measures to protect the species are needed. The creation of local community-based management and bi-national agreements between countries at both ends of migration routes are some of the measures that will likely bring desirable conservation outcomes.

Supplementary Material

The supplementary materials referred to in this article can be found at journals.cambridge.org/bci

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Supplementary Material

Seasonal abundance and breeding habitat occupancy of the Orinoco Goose (*Neochen jubata)* in western Brazilian Amazonia

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Contents

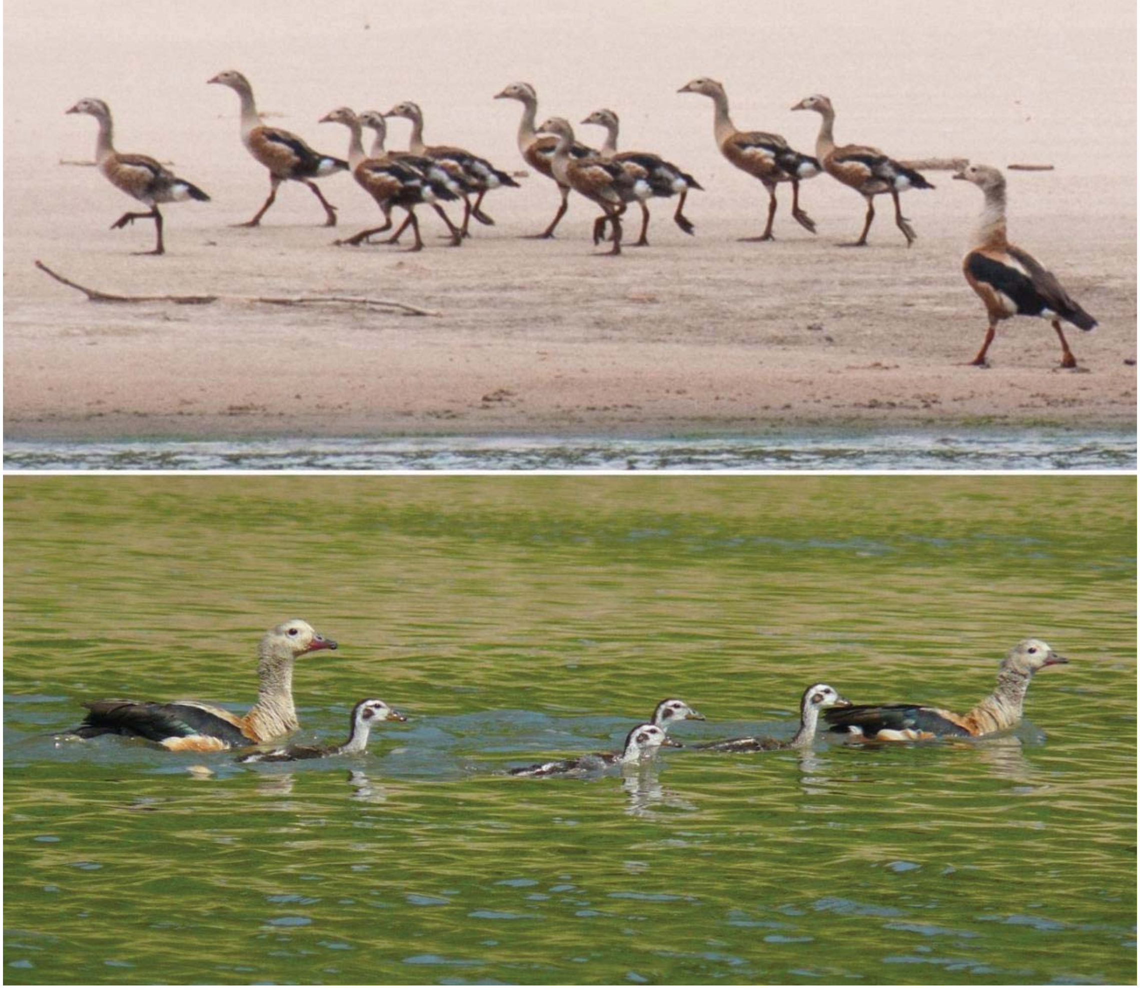

Figure S1. Goslings with parents, at two distinct development stages: downy juvenile (bottom) and fledgling juvenile stage (top).

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