



Logging and indigenous hunting impacts on persistence of large Neotropical animals

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15 **ABSTRACT**

16 Areas allocated for industrial logging and community-owned forests account for over 50% of all
17 remaining tropical forests. Landscape-scale conservation strategies that include these forests are
18 expected to have substantial benefits for biodiversity, especially for large mammals and birds
19 that require extensive habitat but that are susceptible to extirpation due to synergies between
20 logging and hunting. Additionally, their responses to logging alone are poorly understood due to
21 their cryptic behaviour and low densities. In this study, we assessed the effects of logging and
22 hunting on detection and occupancy rates of large vertebrates in a multiple-use forest on the
23 Guiana Shield. Our study site was certified as being responsibly managed for timber production
24 and indigenous communities are legally guaranteed use-rights to the forest. We coupled camera
25 trap data for wildlife detection with a spatially-explicit dataset on indigenous hunting. A multi-
26 species occupancy model found a weak positive effect of logging on occupancy and detection
27 rates, whilst hunting had a weak negative effect. Model predictions of species richness were also
28 higher in logged forest sites compared to unlogged forest sites. Density estimates for jaguars and
29 ocelots in our multiple-use area were similar to estimates reported for fully protected areas.
30 Involvement of local communities in forest management, control of forest access, and nesting
31 production forests in a landscape that includes protected areas seemed important for these
32 positive biodiversity outcomes. The maintenance of vertebrate species bodes well for both
33 biodiversity and the humans that depend on multiple-use forests.

34 **KEYWORDS:** bush meat; subsistence hunting; occupancy model; production forests; selective
35 logging; reduced-impact logging; wildlife management; Iwokrama

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3 36 MANAGED FORESTS can extend the formal “conservation estate” beyond the boundaries of
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5 37 protected areas (e.g., Clark & Poulsen 2009; Putz et al. 2012; Edwards et al. 2014a). For tropical
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8 38 forests managed principally for timber, the magnitude of this conservation benefit depends on the
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10 39 policies and practices implemented during timber harvests and in the periods between harvests.
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12 40 Control of forest access is of especially high priority to curb the illegal hunting that has
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14 41 contributed to global declines of vertebrate populations (Redford 1992, Wilkie *et al.* 2000,
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16 42 Laurance & Edwards 2014, Bicknell *et al.* 2015). Faunal loss may affect forest productivity, tree
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18 43 species composition, and the food security of forest-dependent people (Levi *et al.* 2009, Dirzo *et*
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20 44 *al.* 2014).

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25 45 Hunting pressure in tropical timber concessions is especially high due to the improved
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27 46 access provided by logging roads and the influx of forestry workers, miners, and other people
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29 47 (Robinson & Bennett 2000, Wilkie *et al.* 2000). The largest vertebrates are the preferred prey of
30
31 48 most human hunters and the first to decline due to their characteristically low fecundities and
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33 49 sparse populations (Peres 2000). Their population recovery rates are also impeded if their home
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35 50 ranges are reduced subsequently by forest conversion to croplands or pastures (Morrison *et al.*
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37 51 2007). Depletion of large vertebrates may directly affect recruitment and survival of many tree
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39 52 species through loss of their dispersal services (Harrison *et al.* 2013, Caughlin *et al.* 2014). For
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41 53 example, tapirs (*Tapirus spp.*), the largest mammal native to the neotropics, and an often over-
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43 54 hunted herbivore, are important seed dispersers for many large-seeded tree species such as
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45 55 *Manilkara zapota*, a canopy tree species commercially important for both its timber and latex
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47 56 (Fragoso & Huffman 2000, O’Farrill *et al.* 2013). The ability of vertebrates to persist in and
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49 57 move around tropical forests is thus of great importance for natural regeneration processes that
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3 58 contribute to the recovery of timber species and carbon stocks in managed forests (Jansen &
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5 59 Zuidema 2001, Rosin 2014, Osuri *et al.* 2016).
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9 60 Strictly protected areas are and will remain critical for conservation but many are not
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11 61 large enough to maintain viable populations of vertebrates with large home ranges, including
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13 62 apex predators (Cantú-Salazar & Gaston 2010, Peres 2005). As selective logging leaves most of
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15 63 the forest intact, large production forests adjacent to protected areas will allow continued animal
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17 64 movements and thereby reduce fragmentation (Elkin & Possingham 2008, Edwards *et al.* 2014).
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19 65 Despite the critical ecological importance and threatened status of many large vertebrates,
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21 66 knowledge about the impacts of logging on this group of animals remains limited (Vetter *et al.*
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23 67 2011). For example, a recent meta-analysis of logging impacts on biodiversity that utilized 48
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25 68 studies included only one study on large vertebrates (Burivalova *et al.* 2014).
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31 69 Given that the majority of timber concessions experience substantial hunting pressure, it
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33 70 is difficult to untangle the effects of logging from those associated with hunting (Vetter *et al.*
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35 71 2011, Brodie *et al.* 2015). Hunting is an especially complex issue where subsistence hunting by
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37 72 indigenous people is legally sanctioned and managed forests abut or overlap with their traditional
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39 73 lands. This study was able to address both of these issues because it was conducted in a
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41 74 sustainable use reserve co-managed by a non-governmental organization (Iwokrama
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43 75 International Centre; <http://iwokrama.org>) and local indigenous communities (North Rupununi
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45 76 District Development Board; <http://nrddb.org>) who jointly develop forest use policies.
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48 77 Iwokrama's forest operations were certified by the Forest Stewardship Council (FSC) as
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50 78 responsible managed, access and hunting by non-indigenous people is strictly controlled, and the
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52 79 permanency of the forest estate is nationally legislated. We assess the biodiversity outcomes
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54 80 specific to large vertebrates that derive in part from these resource-use policies.
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3 81 We partition the effects of selective logging and subsistence hunting by indigenous
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6 82 people on large terrestrial vertebrates (> 1 kg) with animal surveys using camera traps and
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8 83 spatially explicit surveys of indigenous hunting. We apply a hierarchical multi-species
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10 84 occupancy model to our binary detection data that enables us to account for species-specific
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12 85 differences in detectability associated with behaviour and abundance (Iknayan *et al.* 2014). This
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14 86 statistical method quantifies the impacts of both logging and hunting on the occupancy state of
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16 87 large vertebrates in a lowland neotropical forest in Guyana that is known to harbour substantial
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18 88 populations of game animals such as tapirs (*Tapiris terrestris*), deer (*Mazama spp.*), giant
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20 89 armadillos (*Priodontes maximus*), paca (*Cuniculus paca*), peccaries (Tayassuidae), as well as
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22 90 large predators such as jaguars (*Panthera onca*) and pumas (*Puma concolor*) that are rare or
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25 91 absent in degraded forests (Lim & Engstrom 2005, Read *et al.* 2010).
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3 92 **METHODS**
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7 93 STUDY AREA – Field work was conducted in Iwokrama Forest in central Guyana (4-5° N, 58.5-
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9 94 59.5°W; Fig. 1), a 370,000-ha conservation area. Iwokrama is zoned into a sustainable-use area
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11 95 where selective logging and other resource-use activities are permitted (e.g., ecotourism and non-
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13 96 timber forest product extraction), a wilderness preserve where anthropogenic disturbances are
14
15 97 prohibited, and a titled indigenous community resource-use area. This moist tropical rainforest,
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17 98 with small areas that are seasonally flooded, is located on the Guiana Shield and receives 2693
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19 99 mm of annual rainfall with a marked September - November dry season (<150 mm month⁻¹;
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21 100 Bovolo *et al.* 2012). The area is characterized by highly weathered and nutrient-poor soils, slow
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23 101 canopy dynamics, and high forest biomass as a result of high densities of trees of species with
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25 102 high density wood that mostly produce large seeds (Hammond 2005, Malhi *et al.* 2009). The
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27 103 canopy of these species-rich forests is dominated by *Catostemma spp.*, *Eperua falcata*,
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29 104 *Eschweilera spp.*, *Swartzia leiocalycina*, *Mora excelsa*, *Carapa guianensis*, and *Chlorocardium*
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31 105 *rodiei* (ter Steege 2000). Iwokrama is part of one of the least fragmented lowland tropical
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33 106 rainforests in the Americas and supports an intact community of large vertebrates (Watkins
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35 107 2010; Fig. 2).
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43 108 Timber harvesting operations in Iwokrama followed reduced-impact logging (RIL)
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45 109 standards that included a pre-harvest inventory, liana cutting, road planning, directional felling,
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47 110 and cable winching. Harvesting is carried out with a 60-year harvest cycle and a minimum
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49 111 cutting diameter of 40 cm DBH (diameter at 1.3m above the ground). Average harvest intensity
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51 112 in our study area was 12.4 m³ ha⁻¹ (~6 trees ha⁻¹) but was spatially heterogeneous (minimum =
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53 113 9.1 m³ ha⁻¹ and maximum = 16.4 m³ ha⁻¹) with an average of 72 m ha⁻¹ of roads and skid trails
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55 114 (Rodney 2013a). Densities of trees ≥20 cm DBH in 12 ha of permanent sample plots in unlogged
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3 115 forest and 169 ha of plots in logged forests averaged 228 trees ha⁻¹ and 161.4 trees ha⁻¹,
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6 116 respectively (Rodney 2013b). The forest was FSC certified during the study period.
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9 117 Iwokrama is remote, approximately 240 km from the nearest non-indigenous settlement,
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11 118 but accessible by an all-weather dirt road with entry controlled at several checkpoints; these
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13 119 characteristics together lead to minimal hunting other than for subsistence purposes by local
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15 120 indigenous people. Other land-use practices such as swidden agriculture are controlled by co-
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17 121 management protocols negotiated with the Makushi and Wapishana tribes, who have utilised
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19 122 these forests for thousands of years (see Plew 2005, Read *et al.* 2010, Luzar *et al.* 2011 for a
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21 123 detailed description of the biophysical and social environments).
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26 124 CAMERA TRAP DATA – A total of 52 camera-trap stations were monitored in June-August
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28 125 2011 with 27 in logged and 25 in an adjacent unlogged forest (Fig. 1). The unlogged forest is a
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30 126 6000 ha contiguous buffer zone for the 5747 ha logged area. Timber was harvested during 2007-
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32 127 2011, with the majority completed prior to the study. Camera trap stations (Cuddeback[®] Capture,
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34 128 Non-typical Inc.) were arranged 1-1.5 km apart at sites with signs of animal activity (e.g. animal
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36 129 tracks, scat) to increase chances of photo captures. Each station comprised two cameras installed
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38 130 on opposite sides of the presumed animal path to increase captures and to buffer against camera
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40 131 failure. The effective sample area of each camera-trap station was assumed to be a circle with a
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42 132 diameter of 1.5 km (see TEAM Network 2011). Frames were captured 24 hours per day with a 1-
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44 133 min delay between exposures with the date and time recorded. Consecutive photographs of the
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46 134 same species at the same site were considered new individuals when there was at least a 1-hour
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48 135 interval between “captures”, except for when individuals were identifiable by unique markings
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53 136 (following Bowkett *et al.* 2007). Due to limitations on equipment and personnel, cameras were
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3 137 deployed sequentially, first in the logged forest and immediately after in the adjacent unlogged
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6 138 forest. Cameras were active for 30-33 days at each site (i.e., 1613 trap nights).
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9 139 We used spatially explicit capture-recapture models (SECR) to estimate densities of
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11 140 species with uniquely identifiable individuals across the entire multiple use area surveyed
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13 141 (jaguars and ocelots; Gopalaswamy *et al.* 2012) and mean camera trapping rates as proxies for
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15 142 densities between logged and unlogged sites for all species (Rovero & Marshall 2009). The
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17 143 SECR density estimates for jaguars and ocelots were not partitioned into logged and unlogged
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19 144 forests due to the large home ranges of these carnivores (e.g. jaguars >10 km²; Rabinowitz &
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21 145 Nottingham 1986, Maffei *et al.* 2011), and the contiguous spatial nature of the logged and
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23 146 unlogged forests. Our goal of estimating density is to compare overall SECR density estimates in
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25 147 the multiple-use area from our study with protected forests with little to no anthropogenic
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27 148 disturbance.
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33 149 HUNTING DATA – Survey data on animal kills by hunters from the indigenous community
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35 150 within Iwokrama Forest were collected from 2007-2010 as part of a wider regional study on
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37 151 subsistence livelihood strategies (see Read *et al.* 2010, Luzar *et al.* 2011, Fragoso *et al.* 2016).
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39 152 Hunting surveys were administered to every household in the community by locally recruited
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41 153 indigenous technicians who were residents of the community and trained by project researchers.
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43 154 A hunting record consisted of a hunter ID, the spatial location of the kill site identified by the
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45 155 hunter on a topographic map, and the species hunted. Quality control checks were carried out
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47 156 throughout the data-collection process to identify mistakes and potential falsification of self-
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49 157 reported hunting events. For a discussion of the strengths and limitations of these self-reported
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51 158 hunting data, see Luzar *et al.* (2011).
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3 159 We filtered the hunting records to include only large terrestrial vertebrates (> 1 kg;
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6 160 Appendix S1 - Table S1), which led to the exclusion of mainly aquatic species (e.g., river
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8 161 turtles). Kill sites marked by the hunters on a topographic map were used to estimate hunting
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10 162 rates for 400 m x 400 m grid cells across a minimum convex polygon (39,000 ha) that captured
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12 163 all kills as well as the logged and unlogged forest areas where camera traps were deployed. Total
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14 164 number of kills for the entire study period was then extracted for each grid cell and used as a
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16 165 response variable. As our question here concerns how hunting affects wildlife occupancy, we
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18 166 used total number of kills as a cumulative metric of spatial hunting rates across the 21 months of
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20 167 data from the livelihood study. We used a negative binomial distribution to account for over-
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22 168 dispersion because the number of kills is heavily skewed towards zero with a few large outliers
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24 169 (Bolker 2008; Appendix S1 - Figure S1). We then predicted mean hunting rate (μ) for each grid
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26 170 cell (j) as a function of distance from the village within Iwokrama with an integrated nested
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28 171 Laplace approximation (INLA; Lindgren *et al.* 2011) to account for spatial autocorrelation,
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30 172 where ξ_j represents a spatial random effect. Distance (β_{hunting}^1) from the village was the only
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32 173 fixed effect in our hunting model (distance from the nearest road and river did not improve
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34 174 model fit and were excluded in the final model):

$$\log(\mu_j) = \alpha_{\text{hunting}} + \beta_{\text{hunting}}^1 \times \text{Village}_{\text{distance}_j} + \xi_j$$

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45 175 Our analysis improves on recent efforts to decouple hunting and logging effects on wildlife by
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47 176 explicit inclusion of spatially referenced kill locations. This approach contrasts with other studies
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49 177 that relied on categorical classifications of hunting (often just, un hunted vs. hunted) or metrics
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51 178 such as hunter encounter rates (Poulsen *et al.* 2011, Brodie *et al.* 2015). The advantage of
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53 179 predicting a mean hunting rate as a covariate in the occupancy model is that the continuous
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55 180 nature of a hunting rate prevents a loss of statistical power compared to when continuous
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3 181 variables are discretized into binary categories such as “hunted vs. non-hunted” (Gelman & Park
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5 182 2009). One caveat to our hunting rate approach is that our surveys did not contain information to
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8 183 allow us to define the catch-per-unit-effort. If catch-per-effort is high in areas where animal
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10 184 abundance is low, our simple hunt rate could be misleading. However, agent-based simulations
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12 185 of hunting at our study region found that confined hunting territory leads to source-sink meta-
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14 186 population dynamics around villages where forest cover is maintained, potentially leading to
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16 187 relatively constant catch-per-unit-effort (Iwamura *et al.* 2014). Additionally, we found that our
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18 188 model-derived hunt rate led to much better model fit of occupancy models, compared to the
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20 189 simpler metric of distance-from-village (Appendix S2).

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25 190 MULTISPECIES OCCUPANCY MODEL – For our occupancy model, we extracted detection
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27 191 records (present/absent) from the camera trap data and used these binary observations as our
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29 192 response variable. Camera trap location was used to situate each trap in either logged or
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31 193 unlogged forest and to predict hunting rates from our spatially-explicit hunting model. We used
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33 194 standard hierarchical occupancy models that are widely used for wildlife camera trap data
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35 195 (Ahumada *et al.* 2013, Tobler *et al.* 2015, Rich *et al.* 2016). Our model represents a multi-species
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37 196 approach to obtain composite information by estimating occurrence probabilities for each species
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39 197 (Dorazio & Royle 2005). The hierarchical model structure permits distinction between non-
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41 198 detection and true absence by an explicit and formal representation of the data into constituent
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43 199 models of the observations (detections) and of the underlying ecological processes (occupancy;
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45 200 Clark 2005, Royle & Dorazio 2008, Iknayan *et al.* 2014). The advantage of a community-level
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47 201 approach is that parameter estimates for data-poor species are more precise because they borrow
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49 202 strength from data-rich species (Zipkin *et al.* 2010, Pacifici *et al.* 2014). We refer to community-
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51 203 level occupancy as the mean occupancy rate across all species, with species-level occupancy
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3 204 drawn from this global distribution (Royle & Dorazio 2008, Zipkin *et al.* 2010). The point-level
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5 205 occurrence model is specified as a Bernoulli distribution, $z(i, j) = \text{Bern}(\psi_{i,j})$ where $\psi_{i,j}$ is the
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8 206 probability that species i occurs at site j . We accounted for species identity in our models of
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10 207 detection and occupancy using species-level random effects for both the intercept term as well as
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12 208 the parameters that describe effects of hunting and logging. Site levels effects are incorporated
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15 209 into the model linearly on the logit probability scale:

$$\text{Logit}(\psi_{i,j}) = \alpha_i + \beta_i^{\text{logged}} \times \text{LOGGED}_j + \beta_i^{\text{Hunt}} \times \mu_j$$

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22 210 in which α_i is the intercept term for the occurrence probability of species i in unlogged forests,
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24 211 and β_i^{logged} and β_i^{Hunt} are parameters that capture the effects of logging and hunting pressure
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27 212 for species i . LOGGED_j indicates whether a grid cell is located in logged or unlogged forests and
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29 213 μ_j is the hunting rate predicted by our INLA model. The detection-level model was similar to the
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32 214 occupancy-level model above insofar as it included the same covariates in a logit-transformed
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34 215 linear model, with intercept, logging and hunting parameters estimated as species-level random
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37 216 effects. As an additional metric of community-level response to hunting and logging, we
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39 217 calculated species richness as the sum of species occupancy values at each site.

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42 218 Of the many ways to account for space in this modeling framework, we chose to use
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44 219 spatially-varying covariates to address spatial non-independence; we explicitly modeled the
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47 220 environmental factors that drive variability in the response variable. This approach is desirable
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49 221 because parameters that represent the effect size of these spatially-varying covariates have direct
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52 222 biological interpretations (Burton *et al.* 2012). Another (non-mutually exclusive) approach is to
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54 223 estimate the effect of space with models for between-point spatial autocorrelation (Royle *et al.*
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57 224 2009). We found little evidence for additional spatial autocorrelation in our models once the
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3 225 effects of hunting rate and logging were included (Appendix S3: Description of the spatial vs.
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5 226 non-spatial models) and so we present hierarchical occupancy models with hunting rate as a
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8 227 spatially-varying covariate. We also compared our occupancy model that used hunt-rate derived
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10 228 from our INLA analysis with a model that substituted distance-to-village and found that hunt-
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13 229 rate outperformed distance-from-village as a predictor of occupancy (Appendix S3).

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16 230 We parameterized our models in a hierarchical Bayesian framework, constructed in the R
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18 231 coding platform (R Core Team, 2015) using R-INLA and JAGS (Plummer 2011), with
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20 232 uninformed priors (Appendix S4: model description and complete R and JAGS code). We ran
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23 233 three chains of length 1,500,000 after a burn-in of 500,000, thinned the posterior chains by 2800,
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25 234 and assessed model convergence using the Gelman-Rubin statistic (Gelman & Hill 2007). To
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28 235 assess statistical power, we simulated occupancy data across a range of parameter values and
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30 236 tested whether our sample size was sufficient to estimate parameter values (Appendix S5). We
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33 237 present our data, model, and simulation code as supplementary materials and online in an open
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35 238 access repository to enable the replication of our analysis.

36 37 38 239 **RESULTS**

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41 240 CAMERA TRAP DATA – We captured 270 and 180 independent photographs of 17 and 15
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43 241 species in the logged and unlogged forest, respectively (Fig. 2; Appendix S1 - Fig. S2).
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46 242 Detections were highest for frugivores (e.g. agoutis and trumpeters) and lowest for omnivores
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48 243 and insectivores (e.g. armadillos, tayras, and coatis; Table 1). Tayras and coatis were detected in
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50 244 logged but not unlogged forest. Mean camera trapping rates were 18 times greater in the logged
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53 245 forest for the largest carnivores (jaguars and pumas) and 3 times greater for the largest
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55 246 herbivores (tapirs and red-brocket deer) compared to the unlogged forest (Table1). Animal
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3 247 densities based on uniquely identifiable individuals for jaguars and ocelots across the combined
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5 248 logged and unlogged forests were estimated at 1.72 individuals/100 km² (95% CI; 1.55 – 2.32)
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8 249 and 16.20 individuals/100 km² (95% CI; 6.92 – 26.7), respectively (Table 1). These values are
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10 250 similar to those reported in the literature for protected areas.

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14 251 HUNTING DATA – We recorded 210 spatially unique hunting kill sites for 13 terrestrial species
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16 252 over 21 months of surveys. All species in the hunting data were also detected with camera traps
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18 253 except two tortoise species, accouchi, and white-lipped peccaries that together account for 23%
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20 254 of all reported kills (Appendix S1 - Table S1). Seven species, mainly from the order Carnivora
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22 255 (jaguars, pumas, ocelots, margays, coatis, and tayras) and grey-winged trumpeters, accounted for
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24 256 38% of all photographs but were not recorded in the hunting data. Species with the highest
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26 257 monthly kill rates were agoutis, pacas, and two peccary species (Table 1). Although distance
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28 258 from the village had a non-significant mean effect (-0.0002; 95% CI, -0.0006 to 0.0001), it was a
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30 259 better predictor of hunting intensity than distance from the nearest road or river. The majority of
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32 260 kill sites were <10 km and mostly upstream from the village (Fig. 1; Appendix S1- Fig. S1).
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34 261 Although much of the logged forest was <10 km from the village, it hosted little hunting.
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40 262 MULTISPECIES OCCUPANCY MODEL – Across all species and sites (logged and
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42 263 unlogged forests), detection had a median value of 4.12% (95% CI, 0.4 to 28.91%), and
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44 264 occupancy had a median value of 54.43% (95% CI, 8.36 to 94.01%). Both logging and hunting
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46 265 had relatively small and non-significant effects on occupancy and detection rates (Fig. 3).
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49 266 Logging resulted in a median increase of 8.81% (95% CI, -16.97% to 34.48%) in community-
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51 267 level occupancy. Species-level effects of logging on occupancy were weak and uncertain, with
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53 268 50% CI overlapping zero for most species (Appendix S1 - Fig. S3). Results from our power
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55 269 analysis suggest that if there had been a significantly negative effect of logging on occupancy,
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3 270 we would have had sufficient statistical power to detect it (Appendix S5). Community-level
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5 271 occupancy at the sites with the highest hunting pressure declined by a median value of 25.01%
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8 272 (95% CI, -57.04 to 17.38%) relative to sites that experienced no hunting. Species-level effects of
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10 273 hunting on occupancy were consistently negative for most species, with the strongest (although
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12 274 non-significant) effects on agoutis (Fig. 5; Appendix S1 - Fig. S3). Using posterior samples, we
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14 275 estimate the probability of negative effects of logging and hunting on community-level
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16 276 occupancy as 24.49% and 88.45%, respectively.
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21 277 We estimated median observed species richness per sample site at 10 species (95% CI, 5
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23 278 to 11) in logged forests and 8 species (95% CI, 2 to 12) in unlogged forests (Fig. 6). Compared to
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25 279 logging, there was a greater effect of hunt rate on estimated species richness, with a median of 10
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28 280 species at the sites with no hunting (95% CI, 7 to 12), compared to a median value of 3 species
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30 281 (95% CI, 0 to 6) at the site with the highest hunting rate.
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33 282 Overall, logging was associated with higher community-level detection of large
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35 283 vertebrates by a median value of 1.76% (95% CI, -0.97 to 6.08%). The strongest species-level
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37 284 effects of logging on detection were observed for the three terrestrial cat species (i.e., jaguars,
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39 285 pumas, and ocelots), with a significant positive effect of logging on puma and jaguar detection
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41 286 (Appendix S1 - Fig. S4). Compared to the community-level effect of hunting on occupancy, the
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43 287 community-level effect of hunting on detection was relatively weak (Fig. 3). Similarly, species-
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45 288 level effects of hunting on detection had a median near zero with wide credibility intervals for all
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49 289 species (Appendix S1 – Fig. S4).
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52 53 290 **DISCUSSION** 54 55 56 57 58 59 60

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3 291 Our results shed light on conservation-compatible policies for managed forests for species
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5 292 susceptible to extirpation from anthropogenic impacts due to intrinsic demographic and life
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8 293 history traits correlated with body size (Bodmer *et al.* 1997). The community of large vertebrate
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10 294 species at our study site remained intact in areas subjected to both reduced-impact logging and
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12 295 traditional indigenous hunting. Community partnerships, like the one in this case study, can
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14 296 increase conservation gains through improved forest management while they contribute to local
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16 297 livelihoods and achievement of development aspirations. Although generalisations based on a
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18 298 study in a single logging operation and a single community need to be made with caution
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20 299 (Ramage *et al.* 2013), our results contribute to knowledge about the conservation benefits to
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22 300 large vertebrates of improved forest management. More specifically, the benefits for biodiversity
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24 301 conservation are clear for policies that require RIL and restrict forest access to people without
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26 302 legitimate claims on forest resources (Edwards *et al.* 2012, Putz *et al.* 2012, Bicknell *et al.* 2014).

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29 303 In forests that do not benefit from the community partnerships and ecologically sound
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31 304 management practices employed in Iwokrama Forest, the potential loss of ground-dwelling
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33 305 vertebrates can affect the nutrition of local people, forest dynamics, and biodiversity (Iwamura *et*
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35 306 *al.* 2014). The large-bodied vertebrates that were retained in our study area are especially
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37 307 important in Guiana Shield forests where seeds of most canopy tree species are too large to be
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39 308 dispersed by wind or small animals (Hammond *et al.* 1996). Loss of these dispersers will result
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41 309 in decreased populations of these large-seeded tree species, a guild that accounts for the above-
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43 310 average carbon content of the forests at our study site that is so important for national climate
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45 311 mitigation programs associated with REDD+ (Malhi *et al.* 2009, Johnson *et al.* 2016). From a
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47 312 sustainable timber production perspective, regeneration of commercial timber species depends
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49 313 on the maintenance of these plant-animal interactions due to the high costs of silvicultural
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3 314 interventions to promote the regeneration and growth of commercial timber species (Rosin
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5 315 2014). Avoidance of conversion of production forest to non-forest land uses, which leads to
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8 316 massive biodiversity losses and carbon emissions, is to some extent dependent on the continued
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10 317 regeneration of these commercially important species (Edwards *et al.* 2014).
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14 318 The observed lack of a negative effect of RIL on large vertebrates is in line with other
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16 319 studies on birds, bats, amphibians and primates conducted in Iwokrama Forest (Bicknell & Peres
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18 320 2010, Bicknell *et al.* 2015, Holting *et al.* 2016). Similar to those studies, we attribute our finding
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20 321 to the low intensity of timber harvests coupled with the use of specific harvesting practices that
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22 322 minimize undesirable logging damage. With planned roads and skid trails coupled with
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24 323 directional felling and log extraction by trained workers, much of the area designated for logging
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26 324 suffers no direct impacts from RIL (Arevalo *et al.* 2016) and therefore remains suitable for
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28 325 species that normally avoid disturbed forests. It should be noted, however, that the higher animal
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30 326 detections observed in logged forests, especially of carnivores, might be a result of the changes
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32 327 in forest structure that improves visual animal detection, animals making use of logging roads,
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34 328 and/or potential increases in food resources (Fragoso 1991, Costa & Magnusson 2003).
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40 329 The current level of subsistence hunting in Iwokrama may in time reduce the animal
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42 330 populations within the hunting catchment area, as evident from the negative effect of hunting on
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44 331 detection and occupancy. Nevertheless, our overall results and those from other studies in the
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46 332 same area indicate that hunting at our study site is and has been sustainable (Read *et al.* 2010,
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48 333 Iwamura *et al.* 2014). Hunting may reduce animal abundances in areas that experience the
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50 334 highest hunting rates, but these same areas may also represent favourable habitats for wildlife
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52 335 and continue to receive dispersing individuals from surrounding forests (Mayor *et al.* 2015,
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54 336 Iwamura *et al.* 2016). Thus, repeated kills at specific sites likely reflect both traditional hunter
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3 337 knowledge and locations favoured by their preferred bush meat species. We believe this effect to
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5 338 hold true over time as the hunting data cover multiple years that span the first 4 years of logging
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8 339 during which the 30-year old village experienced a 150% population increase (Iwokrama,
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10 340 unpublished data).

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14 341 The negative effect of hunting on occupancy and detection that we observed perhaps
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16 342 indicates the sensitivity of this region to overhunting. For example, mean camera trapping rates
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18 343 were highest for agoutis, a small bodied rodent that comes to dominate community composition
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20 344 as overall species diversity and animal abundance declines within village hunting zones (Shepard
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22 345 *et al.* 2012). Additionally, the density estimated for jaguars, the apex predators at our study site,
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24 346 across the multiple-use forest, that included both logged and unlogged forests, falls on the lower
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26 347 range of values reported for protected areas (Maffei *et al.* 2011). The low densities of jaguars
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28 348 may indicate larger individual home-ranges that might reflect population reductions of prey
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30 349 species hunted by humans (Novack *et al.* 2005) or inherently low animal densities associated
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32 350 with Guiana Shield forests (Emmons 1984, Eisenberg 1979). Density estimates for ocelots, a
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34 351 meso-predator, in contrast, were similar to those reported for protected areas, 80% higher than
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36 352 the minimum values reported (Di Bitetti *et al.* 2008). The lack of photo captures of white-lipped
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38 353 peccaries, though recorded in the hunting surveys, may reflect the range-wide declines reported
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40 354 for this species (Fragoso 2004, Richard-Hansen *et al.* 2014, Mayor *et al.* 2015).

41 42 43 44 45 46 47 355 **CONCLUSIONS**

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50 356 Our results provide support for the conservation value of managed forests for large
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52 357 vertebrates that are sensitive to human-induced environmental changes (Laurance *et al.* 2012).
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54 358 The policies and practices specific to our study site that enabled such an outcome included: (1)
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3 359 the ability to exclude non-sanctioned uses that can lead to forest cover loss and forest
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6 360 degradation; (2) co-management institutions with indigenous communities who are legally
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8 361 guaranteed access for hunting and other traditional forest uses and benefit financially from the
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10 362 timber business; (3) adherence to high standards of RIL with third-party certification; and, (4)
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12 363 forest zoning so that protected areas equal in size to timber production forests are established in
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14 364 adjacent wilderness reserves. The existence and enforcement of such policies might serve as
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16 365 indicators of good forest management under global conservation initiatives such as REDD+. An
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18 366 outcome that leads to well-managed tropical forests will be good for biodiversity, enhance
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20 367 indigenous people's livelihoods, and contribute to national development, but only where
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22 368 supported by strong policies and effective enforcement.
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28 369 The impact of selective logging on tropical biodiversity is dependent on the policies,
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30 370 practices, and enforcement contexts in which forest management occurs. Logging and other
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32 371 forest uses such as subsistence hunting by indigenous people are important livelihood activities
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34 372 that can be conducted in ways that do not result in losses of forest cover. Control of forest access
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36 373 through road closure coupled with co-management mechanisms with indigenous communities
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38 374 can clearly serve to improve forest management and prevent illegal hunting, unplanned
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40 375 colonization, and deforestation that leads to massive biodiversity loss (Robinson *et al.* 1999,
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42 376 Fimbel *et al.* 2001, Bicknell *et al.* 2015). To better understand the suite of policies that would
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44 377 lead to the most conservation gains in managed tropical forest, future research should aim to
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46 378 quantify wildlife densities across multiple sites governed by a range of policies (Ferraro 2013,
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48 379 Angrist & Pischke 2014).
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23 388 **DATA AVAILABILITY:** The data used in our occupancy model will be archived on the Dryad
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25 389 Digital repository.
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4 625 **Table and Figure legends**

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7 626 **Table 1:** Species photographed in Iwokrama forest arranged by feeding guild (activity period),
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9 627 body size (kg), density (individuals/km²), threatened status (Emmons & Feer 1990, IUCN 2016)
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11 628 and hunting pressure. Hunting rate is based on 21 months of data collection (see methods). Mean
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13 629 camera trapping rates are used as proxies for species abundance and based on independent photo
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15 630 captures over the sample period.

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19 631 **Figure 1:** Study site location overlain with the predicted hunting surface extracted from a model
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21 632 that uses spatial locations of successful kills over 21 months (2007-2010, total number of kills =
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23 633 210). Camera traps were installed in 2011 for 808 camera trap nights in logged forests and 805
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25 634 camera trap nights in unlogged forests. The effective camera trap sample areas were ~ 5747 ha
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27 635 and ~ 6000 ha in logged and unlogged forests, respectively. The indigenous village studied is the
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29 636 only settlement within the sustainable-use reserve. All camera traps outside of the logged forest
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31 637 boundary are located in unlogged forests within Iwokrama. [Inset-map: Guyana is indicated by
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33 638 the dark outline on the South American map, with Iwokrama in the center of Guyana].

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39 639 **Figure 2:** Species captured in the logged forest (A) *Panthera onca* (jaguar), carnivore; (B)
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41 640 *Tapirus terrestris* (lowland tapir), the largest neotropical frugivore; (C) *Mazama americana* (red-
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43 641 brocket deer), browsing herbivore; (D) *Priodontes maximus* (giant armadillo), a rare and cryptic
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45 642 insectivore; (E) *Leopardus weidii* (ocelot), a meso-carivore; (F) *Pecari tajacu*, (collared
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47 643 peccary). Tapirs, deer, armadillos, and peccaries experience substantial hunting pressure across
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49 644 the neotropics.
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3 645 **Figure 3:** Community-level effects of logging and hunting on occupancy and detection. Dark
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5 646 vertical lines represent 95% credible intervals and grey bands represent the 50% credible
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8 647 intervals.

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11 648 **Figure 4:** Probability of detection (a) and occupancy (b) in unlogged forests for all species
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13 649 recorded in camera traps. Lines as in Fig 3.

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17 650 **Figure 5:** Changes in probability of occupancy at the species level across the range of observed
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19 651 hunting rates. Each coloured line represents a single species.

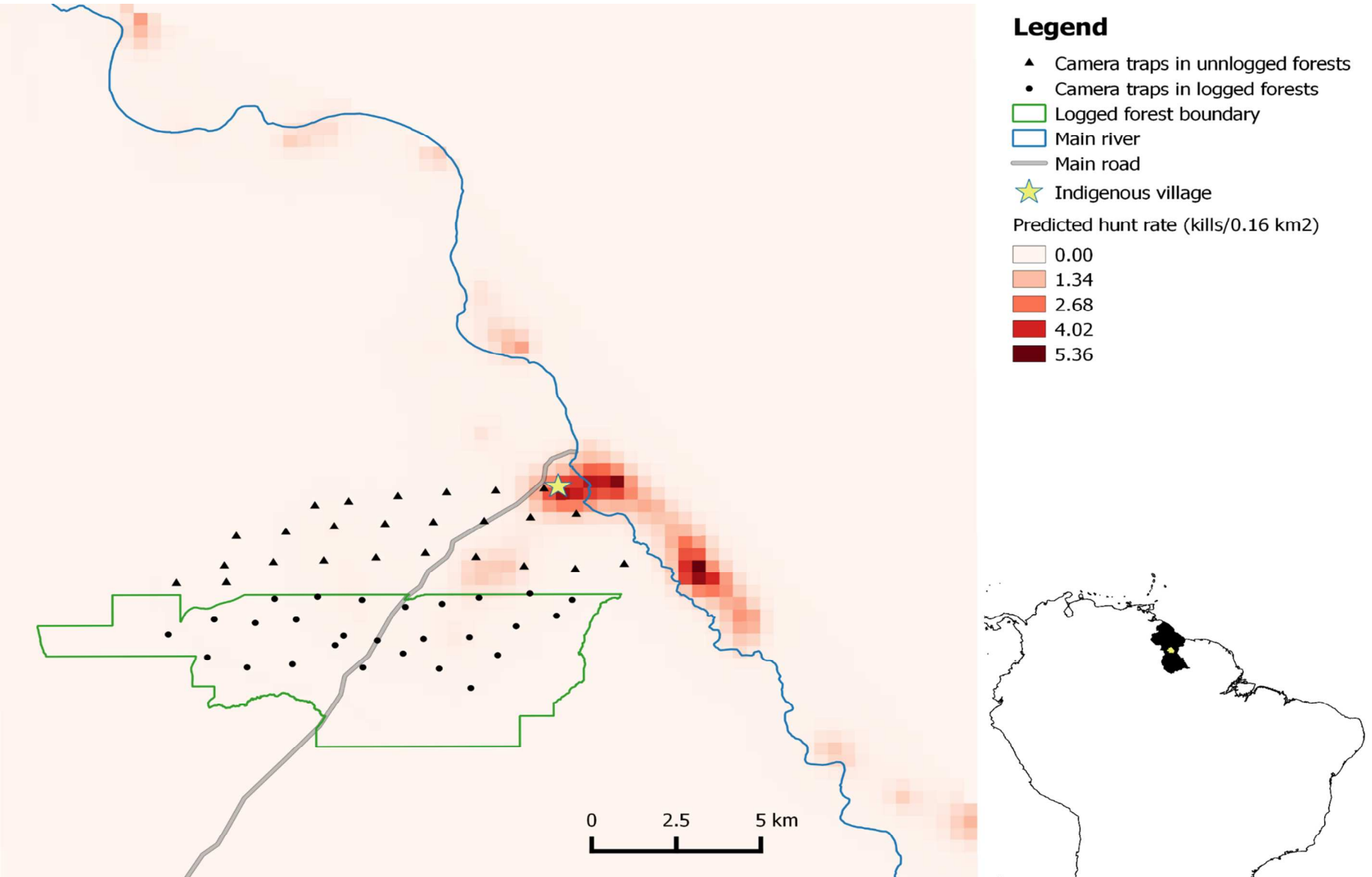
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22 652 **Figure 6:** Predicted species richness for sites in unlogged and unlogged forests. The upper and
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24 653 lower edges of the box plots represent first and third quartiles, the thick black line within each
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26 654 box represents the median value, 'whiskers' represent minimum and maximum observations
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29 655 within 1.5 times of the upper and lower quartiles, and dots represents outliers.

Table 1. Species photographed in Iwokrama Forest by feeding guild (activity period), body size (kg), density (individuals/km²), threatened status (Emmons & Feer 1990, IUCN 2016), and hunting pressure. Hunting rate is based on 21 months of monitoring (see methods). Mean camera trapping rates are used as proxies for species abundance and based on independent photo captures over the sample period.

Scientific name	Common name	Feeding guild (active period)	Size (kg)	Density estimates (individuals/km ²)	IUCN Status	Mean (SE) camera trapping rate		Mean (SE) monthly hunting rate
						Logged	Unlogged	
<i>Crax alector</i>	Black Curassow	Frugivore (diurnal)	2.4 - 3.7	6.90*	Vulnerable	4.33 (± 0.68)	2.61 (± 5.15)	0.24 (± 0.19)
<i>Cuniculus paca</i>	Spotted Paca	Frugivore (nocturnal)	5.0 - 13.0	84.00 - 93.00	Least concern	0.25 (± 5.76)	0.37 (± 1.55)	2.24 (± 0.63)
<i>Dasyprocta leporina</i>	Red-rumped Agouti	Frugivore (diurnal)	3.0 - 5.9	10.50*	Least concern	7.80 (± 9.36)	6.34 (± 9.12)	2.38 (± 1.06)
<i>Dasyopus sp</i>	Armadillo	Insectivore (nocturnal)	2.7 - 6.3	Unknown	Least concern	0.25 (± 1.35)	0.37 (1.55)	0.86 (± 0.28)
<i>Eira barbara</i>	Tayra	Omnivore (diurnal)	2.7 - 7.0	9	Least concern	0.50 (± 1.27)	0 (± 0.00)	No hunting record
<i>Leopardus pardalis</i>	Ocelot	Carnivore (nocturno-crepuscular)	8.0 - 14.5	0.03 - 0.80 (0.16 ± 0.06)	Least concern	2.10 (± 4.40)	0.37 (± 1.17)	No hunting record
<i>Leopardus wiedii</i>	Margay	Carnivore (nocturnal)	3.0 - 9.0	0.01 - 0.05	Near threatened	0.12 (± 0.68)	0.37 (± 1.55)	No hunting record
<i>Mazama americana</i>	Red-brocket Deer	Herbivore (nocturno-crepuscular)	24.0 - 48.0	0.10 - 0.30	Data deficient	1.36 (± 3.12)	0.87 (± 2.60)	0.14 (± 0.10)
<i>Mazama gouazoubira</i>	Grey-brocket Deer	Herbivore (nocturno-crepuscular)	11.0 - 18.0	0.35 - 1.00	Least concern	0.99 (± 1.91)	0.62 (± 1.76)	0.10 (± 0.10)
<i>Myrmecophaga tridactyla</i>	Giant Anteater	Insectivore (diurnal)	22.0 - 39.0	0.12 - 0.41	Vulnerable	0.12 (± 0.68)	0.25 (± 0.98)	0.05 (± 0.05)
<i>Nasua nasua</i>	Coati	Omnivore (diurnal)	3.0 - 7.2	6.20 - 13.00	Least concern	0.12 (± 0.68)	0 (± 0.00)	No hunting record
<i>Panthera onca</i>	Jaguar	Carnivore (nocturno-crepuscular)	31.0 - 158.0	0.01 - 0.11 (0.02 ± 0.003)	Near Threatened	2.60 (± 5.19)	0.12 (± 0.70)	No hunting record
<i>Pecari tajacu</i>	Collared Peccary	Frugivore (diurnal)	17.0 - 35.0	3.00 - 7.00	Least concern	0.74 (± 2.25)	1.12 (± 3.20)	1.33 (± 0.58)
<i>Priodontes maximus</i>	Giant Armadillo	Insectivore (nocturnal)	18.7 - 32.3	0.05 - 0.06	Vulnerable	0.25 (± 0.94)	0.5 (± 1.32)	0.05 (± 0.05)
<i>Psophia crepitans</i>	Grey-winged Trumpeter	Frugivore (diurnal)	1.0 - 1.5	15.30*	Least concern	4.46 (± 8.22)	7.83 (± 11.96)	No hunting record
<i>Puma concolor</i>	Puma	Carnivore (nocturnal)	29.0 - 120.0	0.02 - 0.05	Least concern	4.95 (± 5.10)	0.25 (± 0.98)	No hunting record
<i>Tapirus terrestris</i>	Tapir	Herbivore (nocturno-crepuscular)	227.0 - 250.0	0.20 - 3.70	Vulnerable	2.35 (± 4.23)	0.37 (± 1.55)	0.29 (± 0.10)

Size and density estimates are minimum and maximum values reported in Emmons & Free (1997) and IUCN (2016) respectively; Density estimates with '*' are based on studies in unlogged forests in Iwokrama (Bicknell & Peres 2010). Mean densities (individuals/km²) were estimated for ocelots and jaguars with SECR models with our data shown in parenthesis (means and standard deviations). Mean camera trapping rates is the ratio of independent photo captures to the number of trap days multiplied by 100 (Rovero & Marshall 2009).

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666 **Figure 1.**

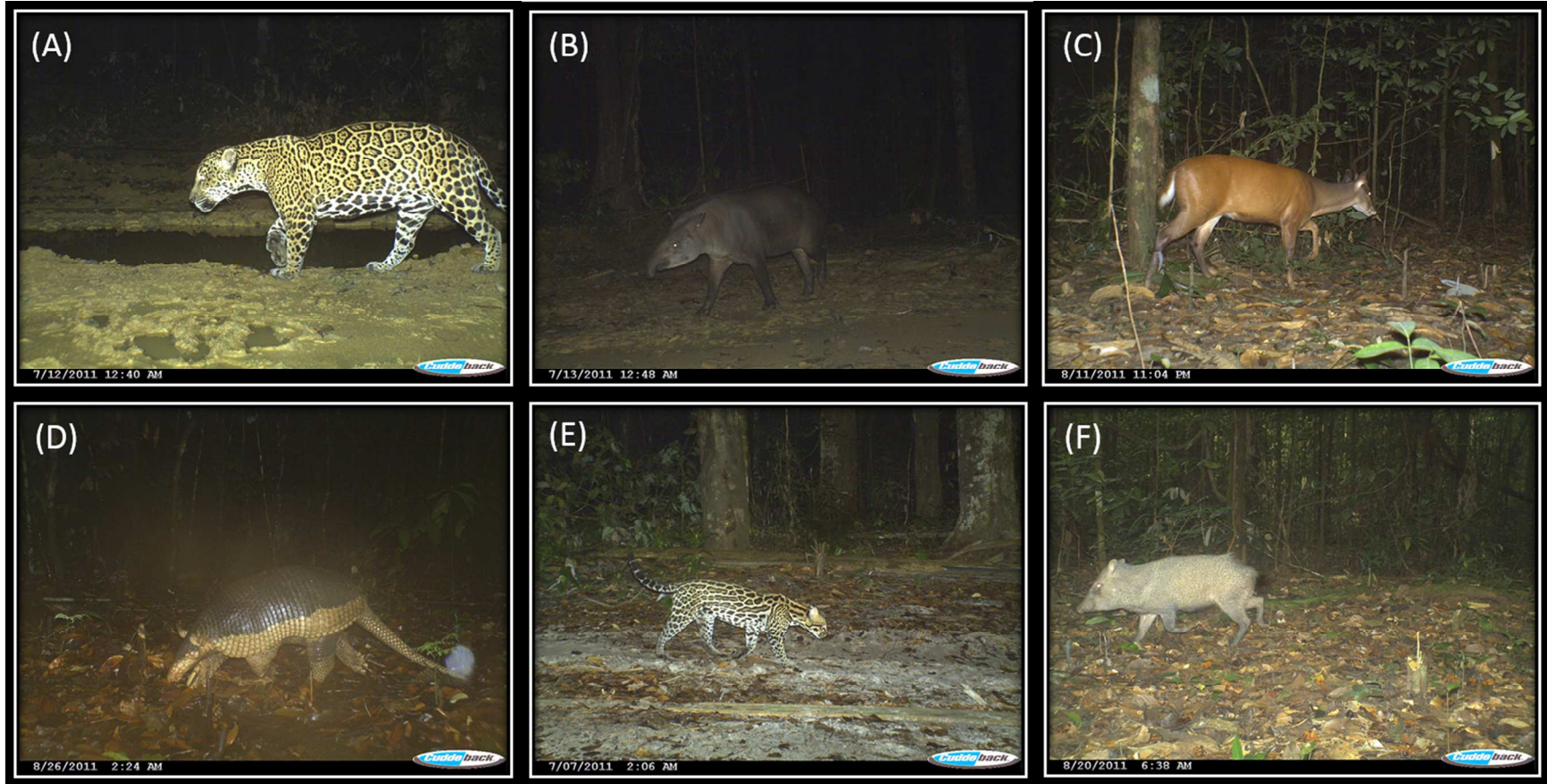
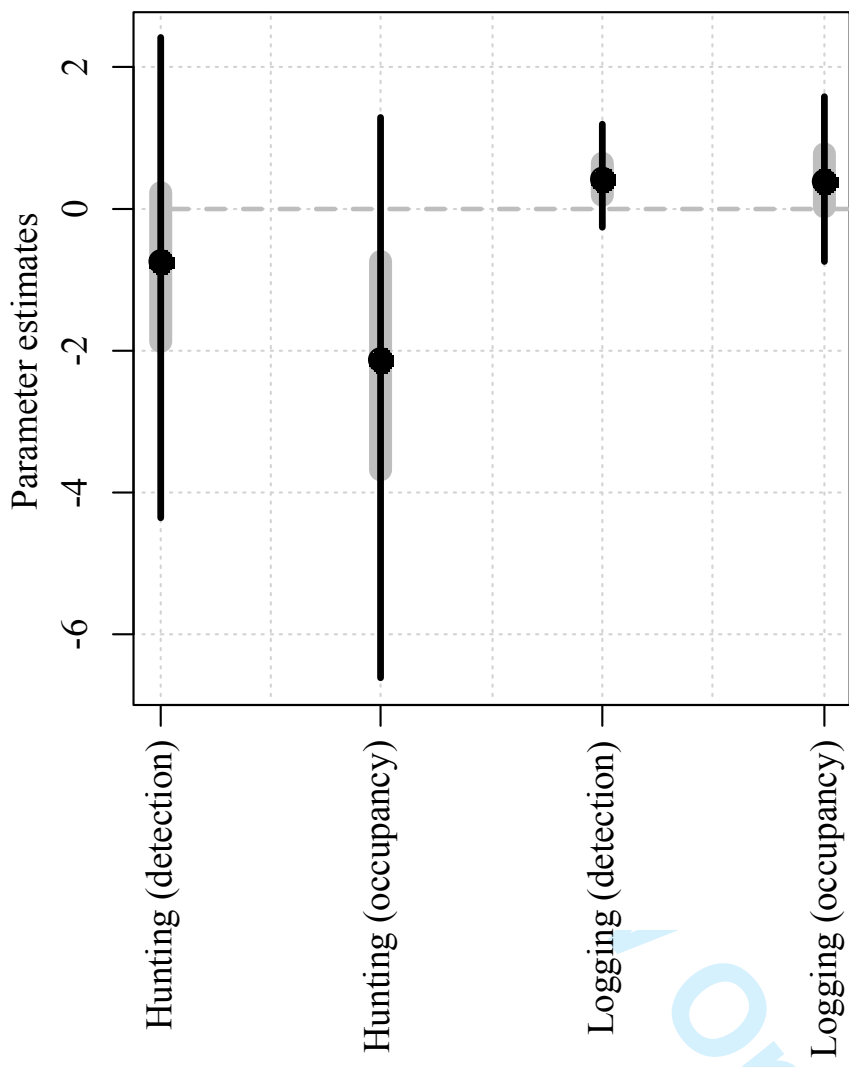


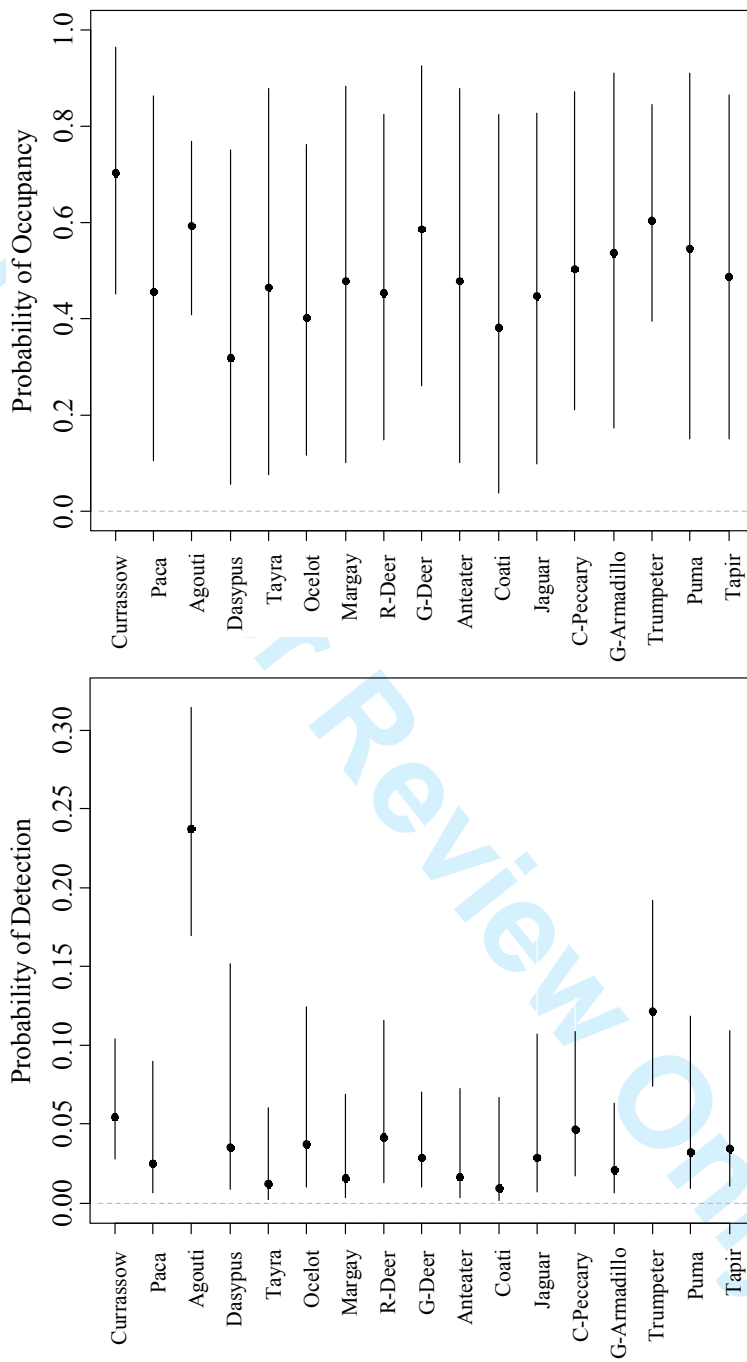
Figure 2.

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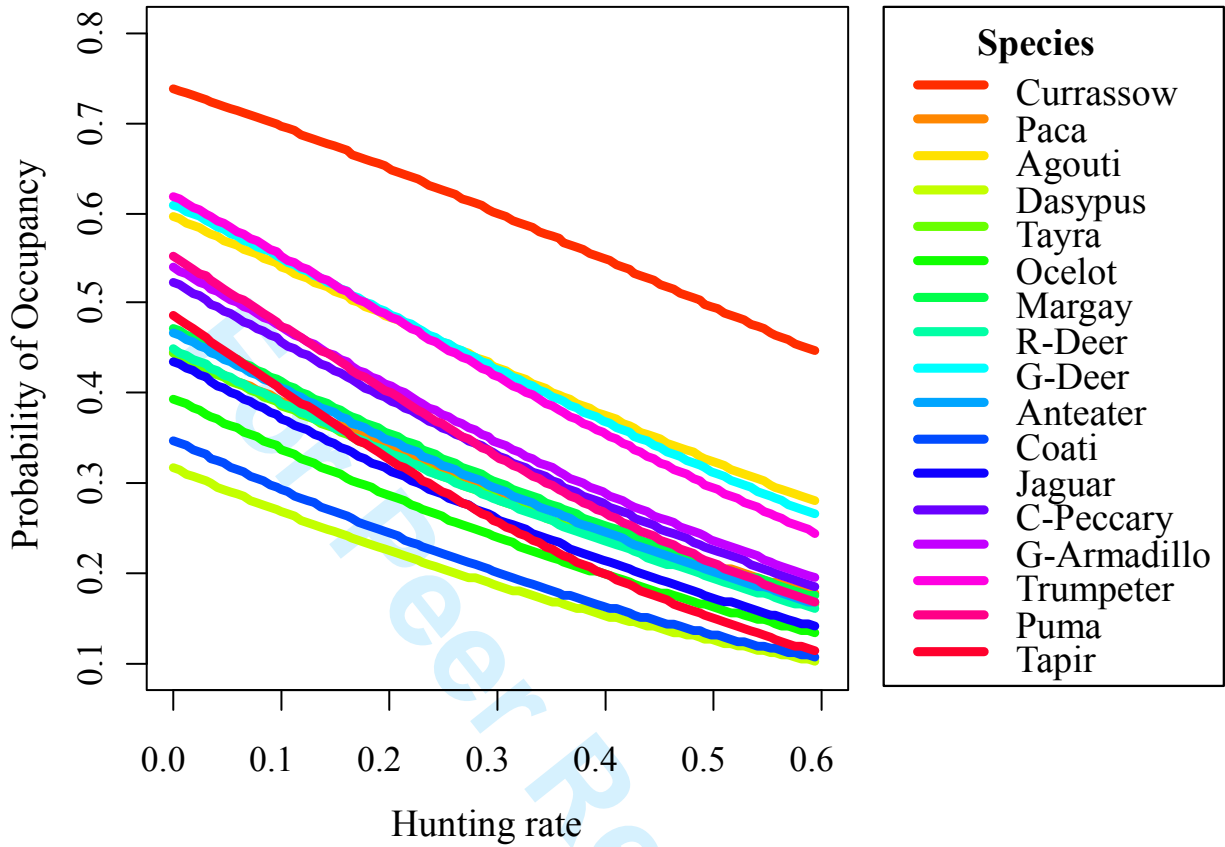
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671 **Figure 3.**



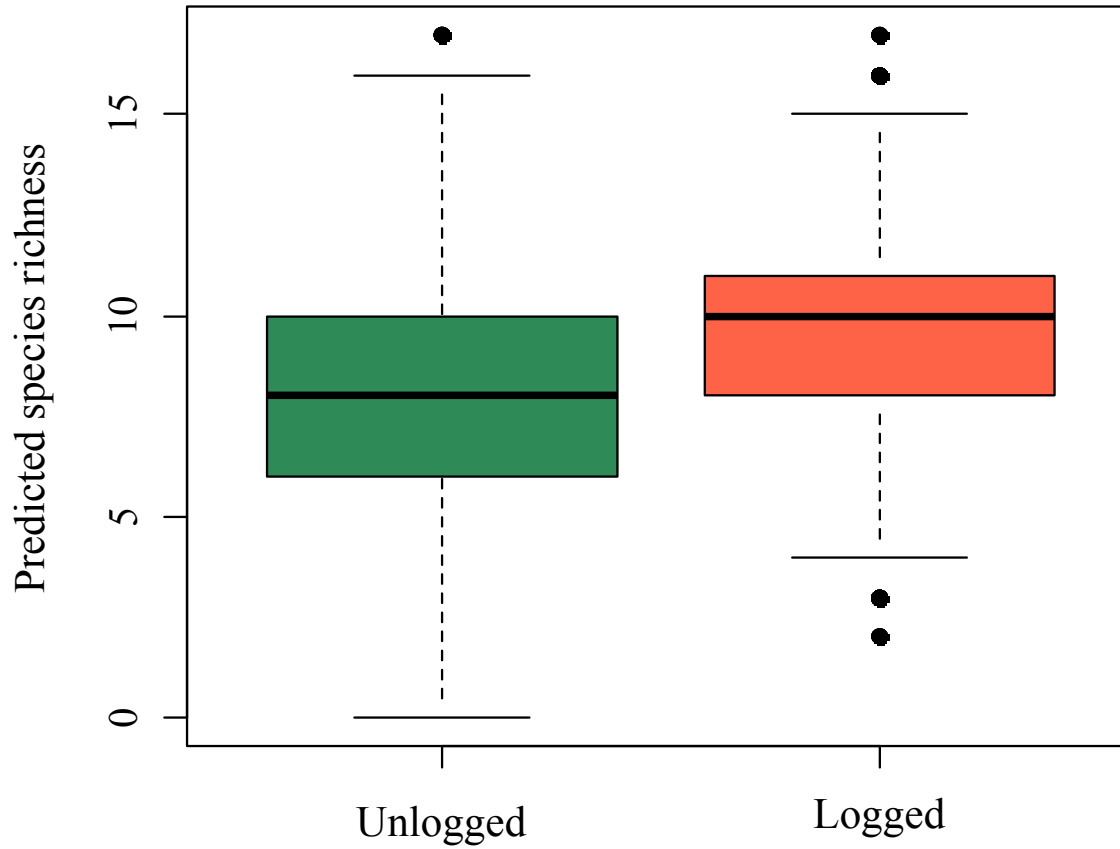
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673 **Figure 4.**



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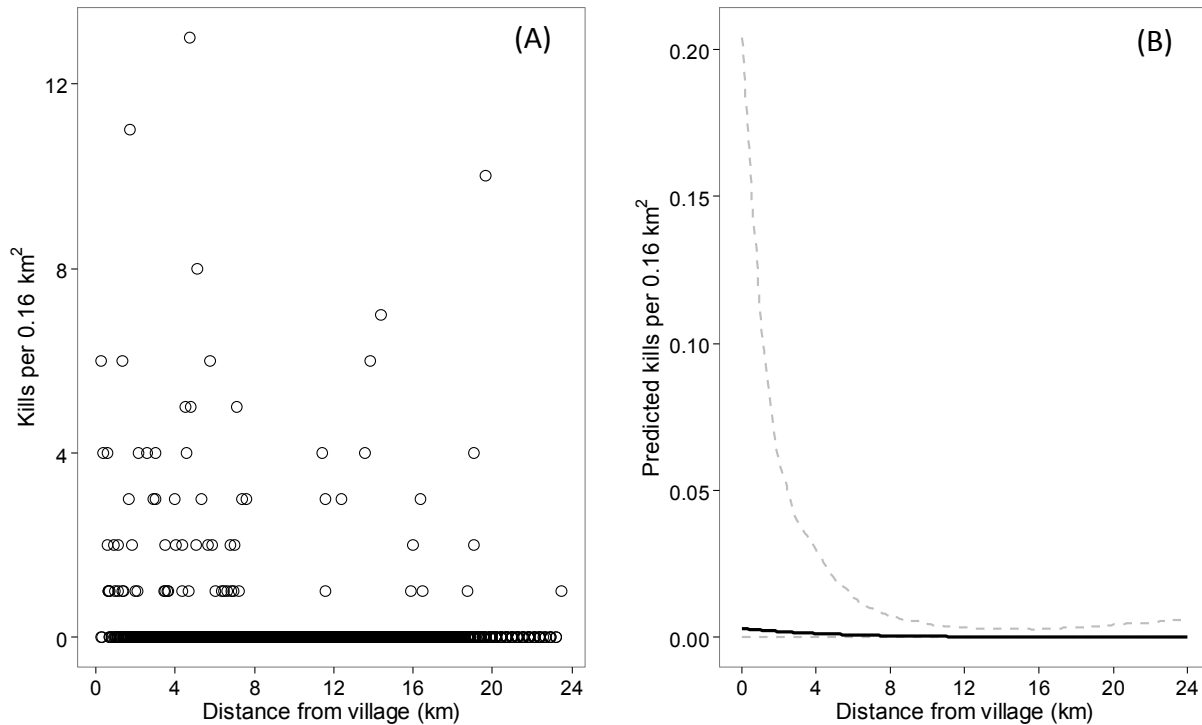
677 **Figure 6.**

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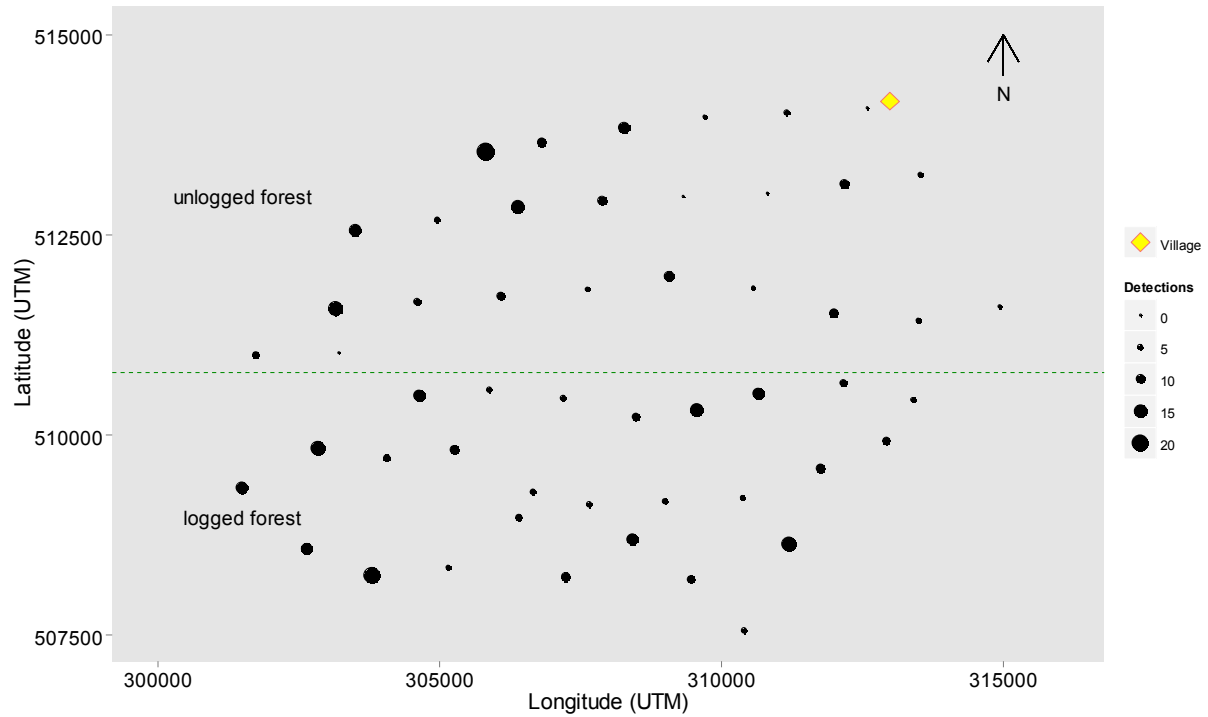
1 **Supplemental Information**2 **Appendix S1: Supplemental figures and tables for main text**3 **Table S1: Terrestrial species killed by hunters over a 21 month period (total number of unique**
4 **kills=210).**

Scientific name	Common name	Feeding guild (active period)	Size (kg)	Density estimates (individuals/km ²)	IUCN Status (2016)	Mean number of kills per month (SE)	Percentage of total kills*
<i>Crax alector</i>	Black Currawong	Frugivore (diurnal)	2.4 - 3.7	6.9	Vulnerable	0.24 (± 0.19)	2.4
<i>Cuniculus paca</i>	Spotted paca	Frugivore (nocturnal)	5.0 - 13.0	84.00 - 93.00	Least concern	2.24 (± 0.63)	22.4
<i>Chelondis sp.</i>	Yellow/red foot tortoise	Frugivore (diurnal)	4.0	5.68	Vulnerable	0.95 (± 0.25)	9.5
<i>Dasyprocta leporina</i>	Red-rumped Agouti	Frugivore (diurnal)	3.0 - 5.9	10.5	Least concern	2.38 (± 1.06)	23.8
<i>Dasyopus sp.</i>	Armadillo	Insectivore (nocturnal)	2.7 - 6.3	Unknown	Least concern	0.86 (± 0.28)	8.6
<i>Mazama americana</i>	Red-brocket Deer	Herbivore (nocturno-crepuscular)	24.0 - 48.0	0.10 - 0.30	Data deficient	0.14 (± 0.10)	1.4
<i>Mazama gouazoubira</i>	Grey-brocket Deer	Herbivore (nocturno-crepuscular)	11.0 - 18.0	0.35 - 1.00	Least concern	0.10 (± 0.10)	1.0
<i>Myoprocta acouchy</i>	Accouchi	Frugivore (diurnal)	1.1 - 1.5	64	Least concern	0.05 (± 0.05)	0.5
<i>Myrmecophaga tridactyla</i>	Giant Anteater	Insectivore (diurnal)	22.0 - 39.0	0.12 - 0.41	Vulnerable	0.05 (± 0.05)	0.5
<i>Pecari tajacu</i>	Collared Peccary	Frugivore (diurnal)	17.0 - 35.0	3.00 - 7.00	Least concern	1.33 (± 0.58)	13.3
<i>Priodontes maximus</i>	Giant Armadillo	Insectivore (nocturnal)	18.7 - 32.3	0.05 - 0.06	Vulnerable	0.05 (± 0.05)	0.5
<i>Tapirus terrestris</i>	Tapir	Herbivore (nocturno-crepuscular)	227.0 - 250.0	0.20 - 3.70	Vulnerable	0.29 (± 0.10)	2.9
<i>Tayassue pecari</i>	white-lipped peccary	Frugivore (diurnal)	25.0 - 45.0	7.58	Vulnerable	1.33 (± 0.98)	3.3

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6 *Ecological characteristics (diet, size and density) extracted from Emmons & Feer (1990) ;*7 *Percentage of kills do not sum to 100% because aquatic species (primarily river turtles;*8 *Podocnemis sp.) hunted are excluded from the analysis.*



9
10 **Figure S1:** Distance-from-village as the main predictor of hunting intensity. *Panel A:* number of
11 kills recorded in the 0.16 km² grid cells. *Panel B:* Predicted hunting rate from the spatial hunting
12 model with 95% credibility intervals (CI) – note the high variation close to the village that
13 declines towards the mean rate of ~ 0.11 kills per 0.16 km² by 10 km from the village.



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15 **Figure S2:** Total number of independent animal detections pooled for all species (N=450) for
 16 808 and 805 camera trap nights in June-August 2011 for logged and unlogged forest,
 17 respectively. The horizontal dashed green line indicates the boundary between unlogged and
 18 forests that was logged between 2007-2011.

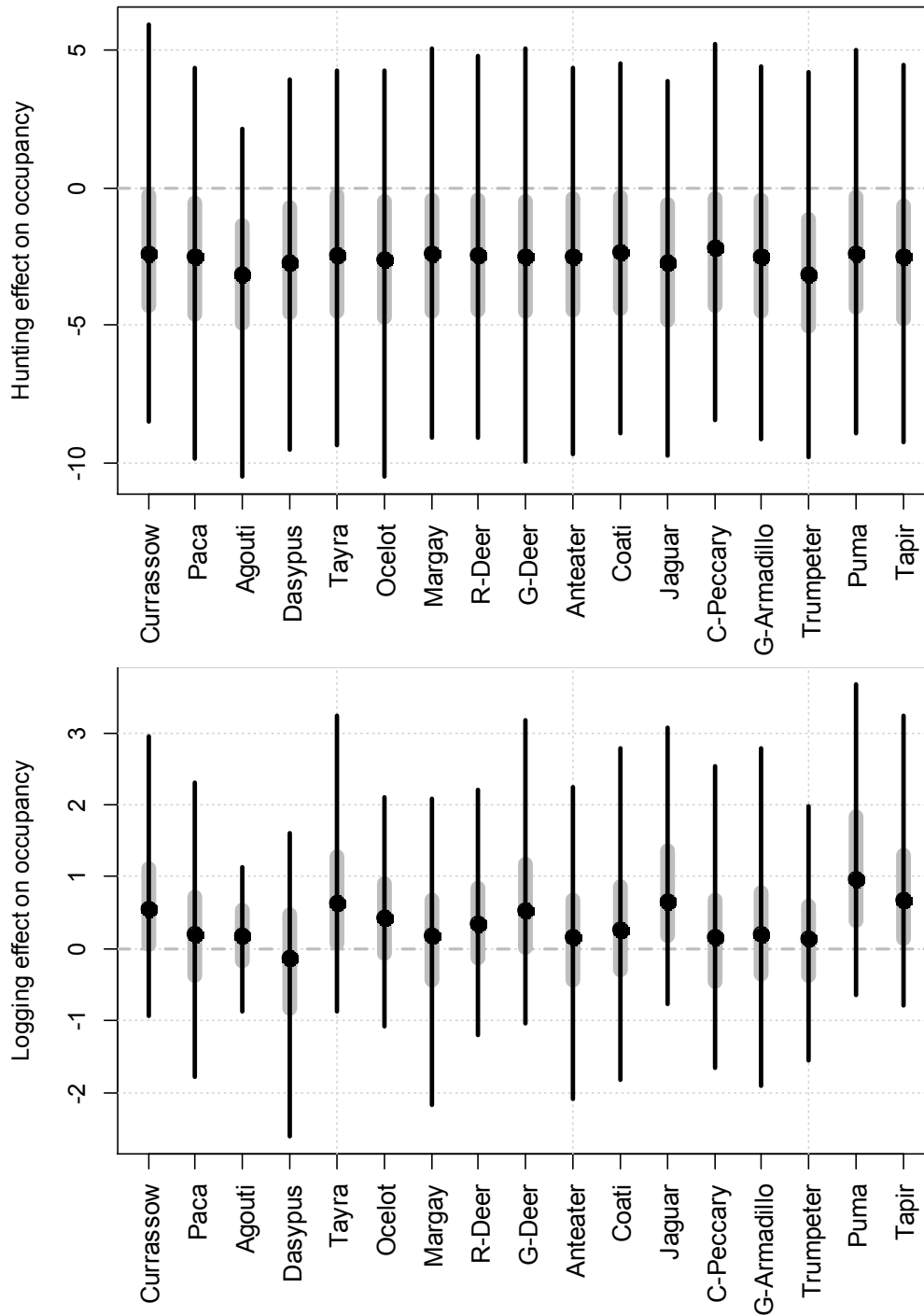


Figure S3. Effects of logging and hunting on species-level occupancy. Thick gray lines indicate 50% CI, and thin black lines indicate 95% CI.

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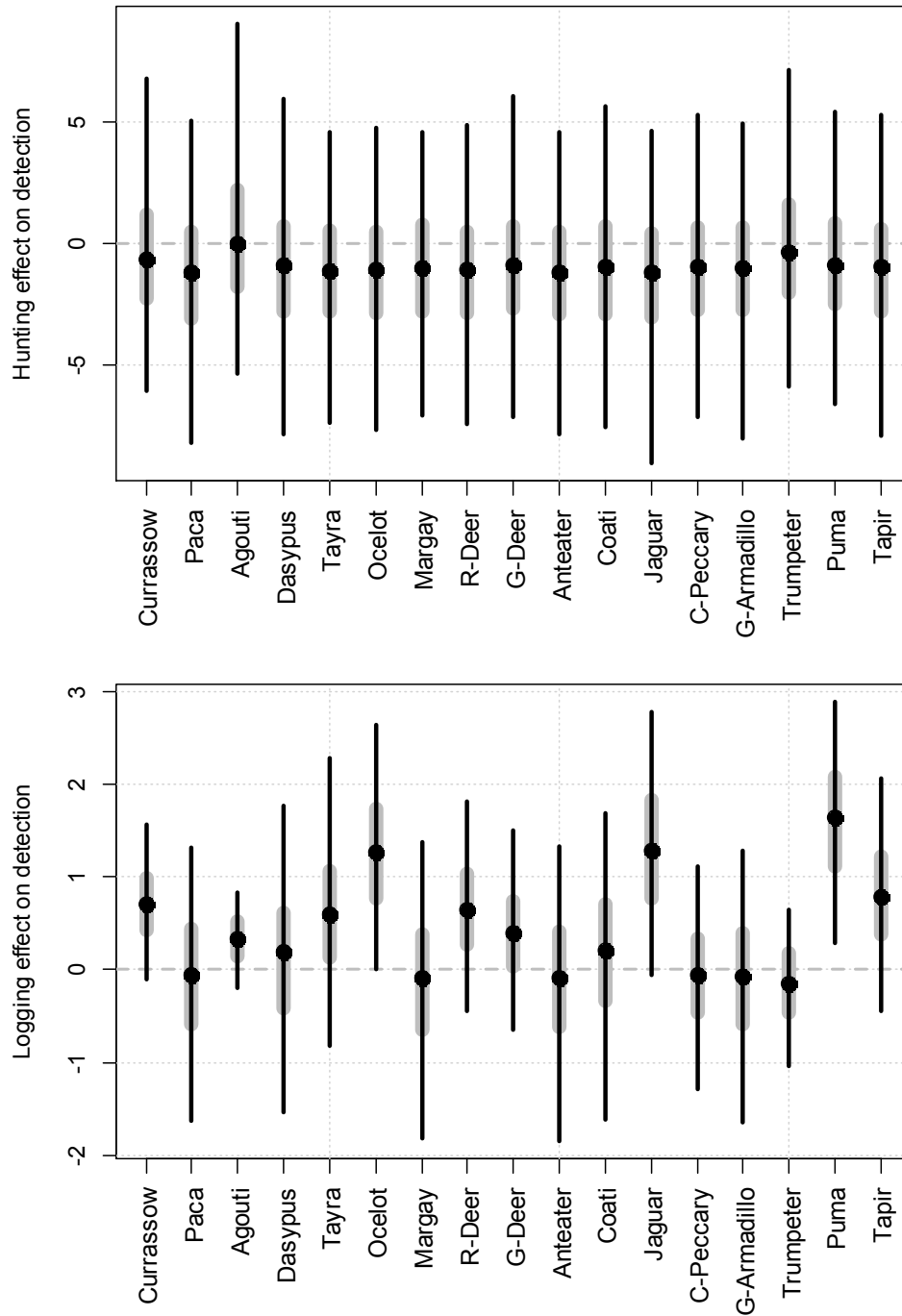


Figure S4. Effects of logging and hunting on species-level detection for the seventeen observed species. Thick gray lines indicate 50% CI and thin black lines indicate 95% CI. Estimates with 95% CI that do not overlap with zero (horizontal dashed gray line) can be considered statistically significant.

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4 21 **Appendix S2: Model results using distance-to-village as a metric of hunting rather than**
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6 22 **hunt rate.**
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9 23 In the main text, we present a multi-species occupancy model that uses a model-derived
10
11 24 hunt rate as a covariate for occupancy and detection. The hunt rate is derived from a spatial
12
13 25 model that includes distance-to-village as a covariate, in addition to accounting for spatial
14
15 26 patterns in number of kills per grid cell (see Fig. 2 in main text). As an alternative, we fit an
16
17 27 occupancy model that included distance-to-village as a metric of hunting, rather than model-
18
19 28 derived hunt rate. Metrics of model selection (DIC and WAIC) revealed that the hunt rate
20
21 29 provided better model fit than distance-to-village (Table S1). Therefore, in the main text, we
22
23 30 present the occupancy model with hunt rate as a covariate. Nevertheless, we found that our main
24
25 31 results (lack of a negative impact of logging on occupancy rates; negative effect of hunting on
26
27 32 occupancy rates) were nearly identical between the model with distance-to-village vs. the model
28
29 33 with hunt rate. Note that a positive correlation between distance-to-village and wildlife
30
31 34 occupancy (Fig. S1), means that camera traps at further distances from the village have higher
32
33 35 wildlife occupancy. In other words, we would expect model-derived hunt rate and distance-to-
34
35 36 village to have opposite effects. In this appendix, Figures S1-S3 present results from the
36
37 37 occupancy model with distance-to-village as a covariate and correspond to Figures 3, 4, and 6 in
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39 38 the main text.
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39 **Table S1:** Deviance information criterion (DIC) and Wantanabe-Akaike information criterion
 40 (WAIC) for models that include hunt rate (estimated from INLA analysis) verses distance-to-
 41 village.

<i>Model</i>	DIC	WAIC
Hunt rate as a covariate	1849.8	9508.6
Distance-to-village as a covariate	1944.5	9821.502

42 *Model selection criteria reveal a better fit of the hierarchical occupancy model with hunt rate,*
 43 *derived from kill data, as a covariate for occupancy and detection compared to the occupancy*
 44 *model with the same structure but with distance-to-village as a covariate instead of hunt rate.*
 45 *Lower values for DIC and WAIC indicate better model fit.*

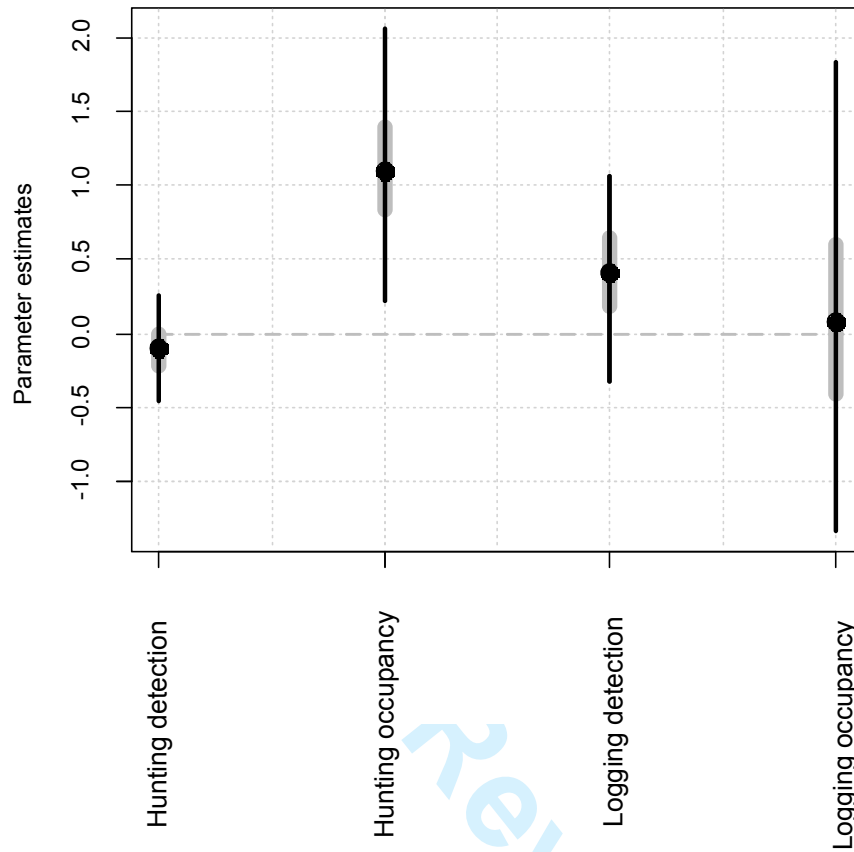
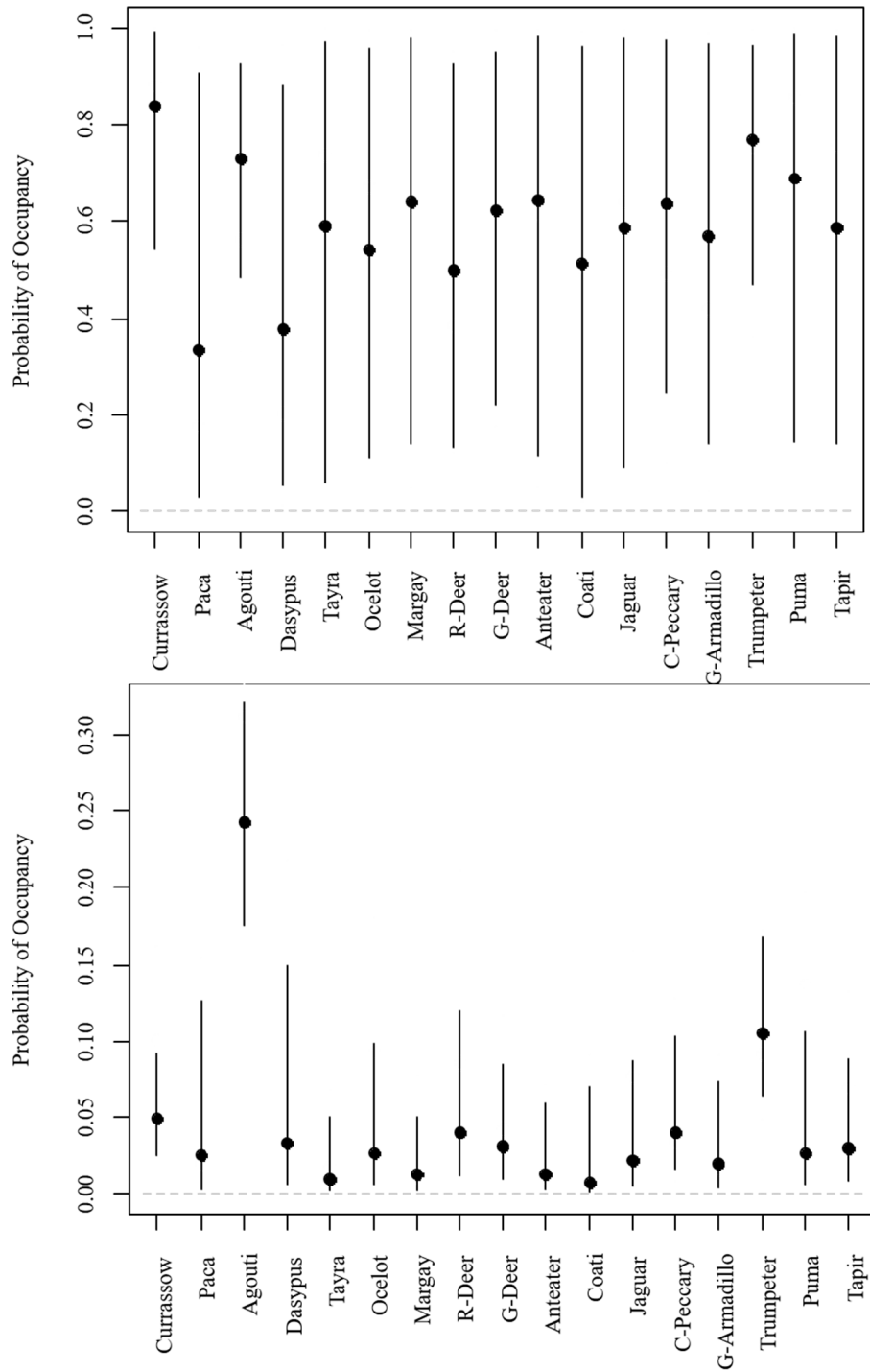


Figure S1: Community-level effects of logging and hunting on occupancy and detection. Dark vertical lines represent 95% credible intervals and grey bands represent the 50% credible intervals. In contrast to the main text, the “hunting” covariate referred to in this figure is distance-to-village, rather than model-derived hunt rate.



62

63 **Figure S2.** Probability of detection (a) and occupancy (b) in unlogged forests for all species

64 recorded in camera traps. Lines as in Fig S1. Note that this figure presents results from an

65 occupancy model with distance-to-village, rather than hunt rate, as a covariate.

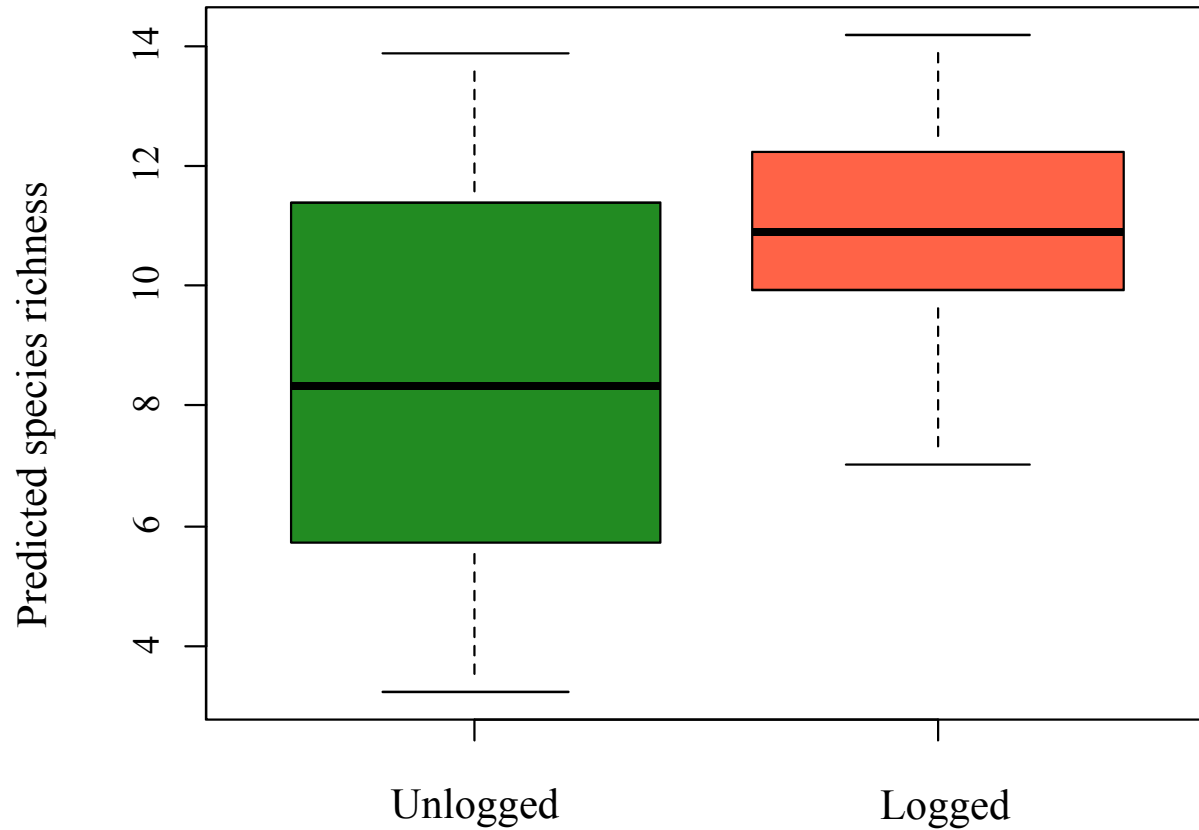
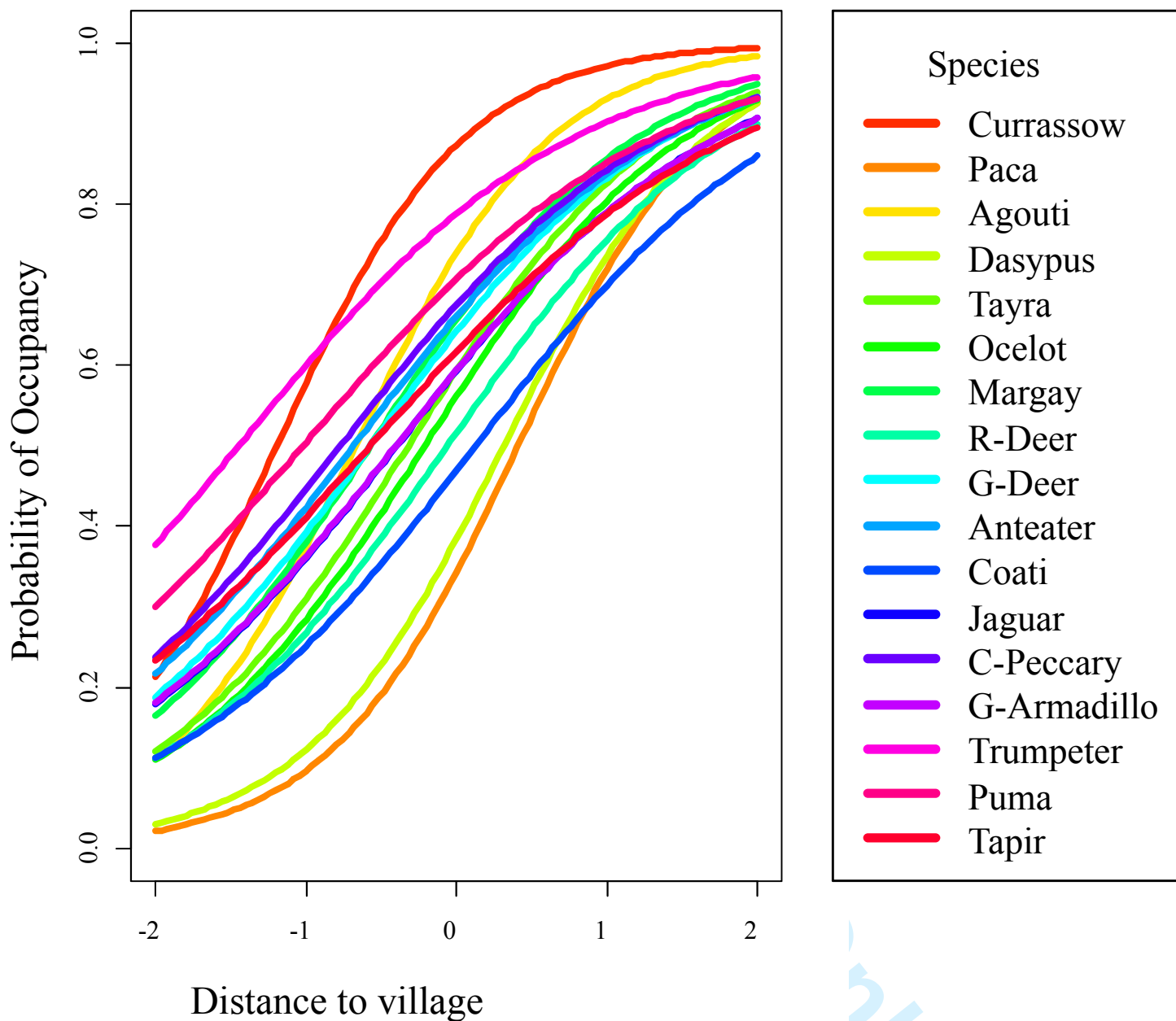


Figure S3. Predicted species richness for sites in unlogged and logged forests. The upper and lower edges of the box plots represent first and third quartiles, the thick black line within each box represents the median value, 'whiskers' represent minimum and maximum observations within 1.5 times the upper and lower quartiles, and dots represents outliers.



102
 103 **Figure S3:** Changes in probability of occupancy at the species level across the range of observed
 104 distances from the village (standardized by centering around the mean and dividing by two
 105 standard deviations). Each coloured line represents a single species.

106 **Appendix S3: Description of the spatial vs. non-spatial models**

107 Similar to many other tropical forestry studies, our design includes blocks of camera traps and
108 potentially risks violating assumptions of spatial independence between neighboring camera trap
109 stations (Ramage *et al.* 2013). To test whether residual spatial autocorrelation, after the effects of
110 hunting rate and logging were taken into account, affects our conclusions, we compared spatial
111 and non-spatial models for occupancy for our wildlife species. Although hierarchical models for
112 wildlife occupancy that account for imperfect detection and include spatial random effects are
113 possible (Johnson *et al.* 2012), preliminary analyses suggested that our sample size was
114 insufficient to parameterize these complex models. Consequently, to examine the effects of
115 space, we explored models with a binary response variable to represent occupancy, coded as “1”
116 if a species was ever detected at a camera trap site and “0” otherwise. We then fit models in
117 INLA (Lindgren *et al.* 2011) for binary detection as a response variable, predicted hunting rate
118 and logged vs. unlogged treatments as fixed effects and species as a random effect. We
119 compared a model that included a spatial random effect with a model that included no spatial
120 effects. If spatial autocorrelation had a significant effect on our model structure, we would expect
121 that (1) effect of logging and hunting rate would differ in the spatial vs. non-spatial model and
122 (2) the spatial model would fit the observed data better than the non-spatial model.

123 We found no evidence that accounting for spatial autocorrelation would change our primary
124 conclusions with similar effect sizes and uncertainty for logging and hunting parameters in both
125 models (Fig. S1). Additionally, the DIC and WAIC values for the spatial vs. non-spatial model
126 were similar (Table S1), suggesting that there is no clear evidence in favor of one model over the
127 other. For these reasons, we present the non-spatial hierarchical model for occupancy in the main
128 text.

129 *Literature cited*

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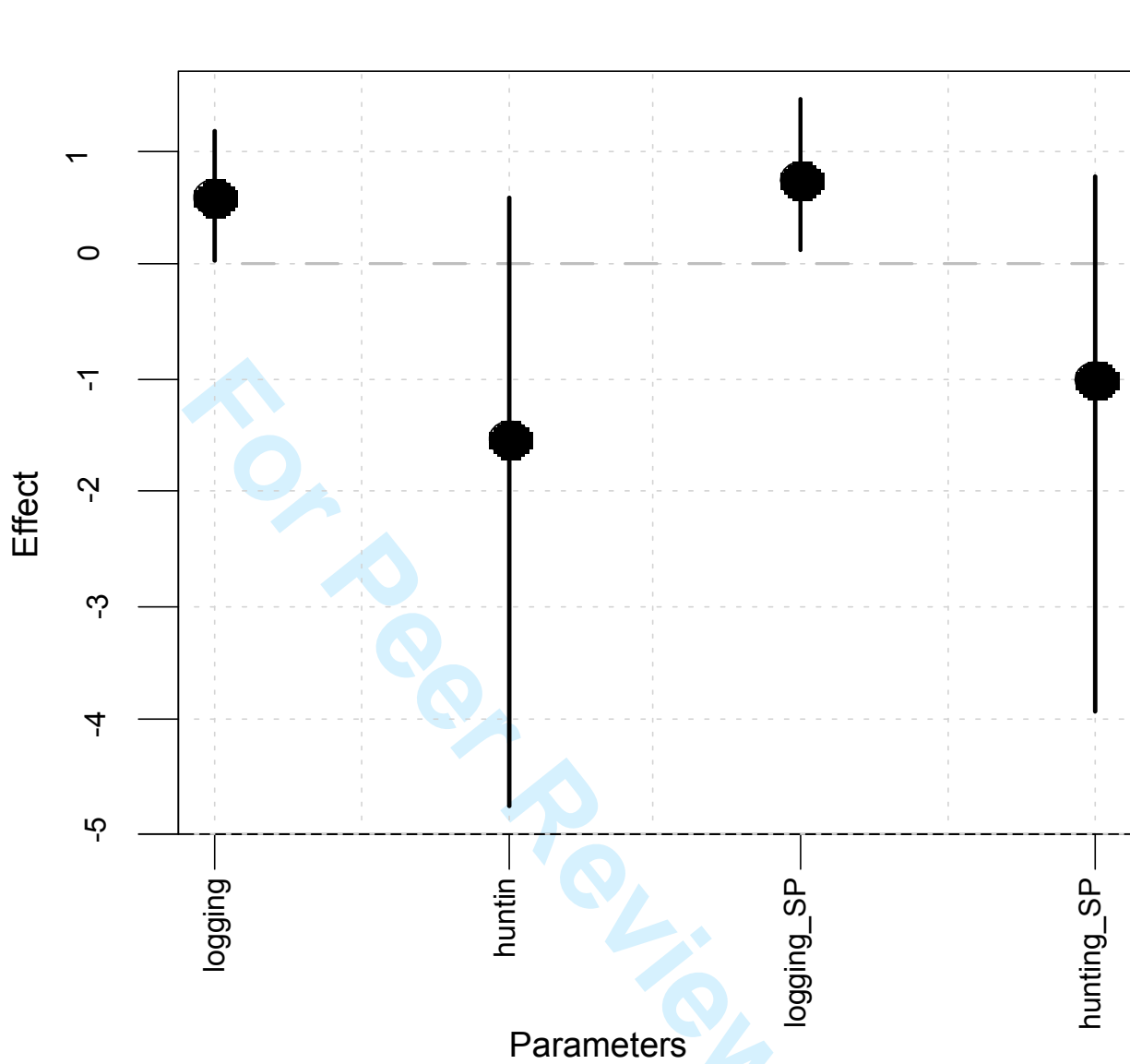
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4 141 **Table S1:** Deviance information criterion (DIC) and Wantanabe-Akaike information criterion
5
6 142 (WAIC) for our spatial and non-spatial models. Model selection criteria reveal minimal
7
8 143 difference between spatial and non-spatial models for wildlife occupancy at our study site.
9
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<i>Model</i>	DIC	WAIC
Spatial	399.72	397.01
Non-spatial	402.97	397.49

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145 **Figure S1:** Mean effect size and 95% credible interval (vertical lines) of effects on logging and
146 hunting from the non-spatial model (left) compared to the spatial model (right, indicated by
147 “SP”).

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4 149 **Appendix S4: Hierarchical community occupancy model – JAGS code**
5

6
7 150 We estimated Bayesian parameters using a Markov Chain Monte Carlo algorithm with
8
9 151 the program JAGS (using the ‘R2jags’ R package) in R for 3 chains of length 1,500,000 after a
10
11 152 burn-in of 500,000 and thinned by 2800. The burn-in discards samples from the analysis drawn
12
13 153 prior to model convergence and thinning help reduce the correlation between neighboring
14
15 154 iterations. Convergence was assessed by examining the Gelman-Rubin statistics for each
16
17 155 parameter estimate (Gelman & Hill 2007). The model code, including the prior distributions is
18
19 156 presented below.
20
21

22
23
24 157 JAGS model code:

25
26
27 158 model {
28
29
30 159 # Prior distributions on the community level occupancy and detection covariates
31
32
33 160 mu.INTERCEPT ~ dbeta (1, 1)
34
35
36 161 LOGGED ~ dnorm (0, 0.001) #Fixed effect of logging on occupancy
37
38
39 162 HUNTING ~ dnorm (0, 0.001) # Fixed effect of hunting on occupancy
40
41
42 163 HUNT_det ~ dnorm (0,0.001) # Fixed effect of logging on detection
43
44
45 164 LOG_det ~ dnorm (0,0.001) # Fixed effect on detection
46
47
48
49
50 165
51
52
53 166 sigma.INTERCEPT ~ dunif(0, 10)
54
55
56 167 tau_INTERCEPT<-1/(sigma.INTERCEPT*sigma.INTERCEPT)
57
58
59
60

```

1
2
3 168      # Community level priors for species random effects
4
5
6
7 169      mu.SP~dbeta(1, 1)
8
9
10 170      sigma.SP~dunif(1, 10)
11
12
13 171      tau_SP <-1/(sigma.SP*sigma.SP)
14
15
16 172      for (i in 1:Nspecies) {
17
18
19 173      p.detect[i] ~ dnorm(logit(mu.SP),tau_SP)
20
21
22 174      INTERCEPT[i] ~ dnorm(logit(mu.INTERCEPT),tau_INTERCEPT)
23
24
25
26 175      }
27
28
29 176      # Estimating true occupancy
30
31
32 177      For (i in 1:Nobs) {
33
34
35 178      logit(psi[i]) <- INTERCEPT[Species[i]] + LOGGED * Site [i] + HUNTING *
36
37
38 179      HUNT_rate [i]
39
40
41 180      z[i] ~ dbern(psi[i])
42
43
44
45 181      # Detection probabilities
46
47
48 182      logit(p[i])<- (p.detect [Species[i]] + HUNT_det * HUNT_rate[i] + LOG_det* Site [i])
49
50
51 183      Y[i] ~ dbinom(z[i] *p[i], J[i])
52
53
54 184      Y.predict[i] ~ dbinom(p[i], J[i])    }
55
56
57 185      }
58
59
60

```

186 **Appendix S5: Power analysis**

187 Our occupancy models suggest that the community-level effect of logging is slightly positive
 188 with an estimated median value of 0.37 (95% CI: -0.72 to 1.57). Thus, we did not find a
 189 significant, negative impact of logging on wildlife occupancy across our community of 17
 190 species. To guard against a Type II error (accepting a null hypothesis that is actually false), we
 191 conducted a power analysis that asks, given our observed rates of occupancy, detection, and our
 192 sample size, what is the probability of estimating a positive effect of logging on occupancy when
 193 the true effect is negative?

194 To answer this question, we simulated 21,480 datasets using a hierarchical model for occupancy
 195 (z) with imperfect detection:

$$\text{Logit}(\psi_{i,j,k,l}) = \alpha_{i,k} + \beta_{i,l}^{\text{logged}} \times \text{LOGGED}_j + \beta_{i,k}^{\text{Hunt}} \times \mu_j \quad \text{Eq. S1}$$

$$z_{i,j,k,l} \sim \text{Bernoulli}(\psi_{i,j,k,l})$$

196 In Eq. S1, the variables LOGGED and μ represent observed logging treatment and hunting rate,
 197 respectively, with one measurement for each of j sites. The intercept parameter (α) as well as the
 198 effect of hunting rate (β^{Hunt}) were drawn as k^{th} value of the posterior distribution for these
 199 estimated parameters for site j and species i . In contrast, the effect of logging (β^{logged}) was
 200 drawn for species i from a normal distribution with a true value, l , of community logging effect
 201 (L^μ) that included twenty values in an evenly-spaced sequence from a strong negative effect (-5)
 202 to a weakly negative effect (-1e-05):

$$\beta_{i,l}^{logged} \sim \text{Normal}(L_l^\mu, \sigma) \quad \text{Eq. S2}$$

203 The reason for replicating different “true” values of the community-level logging effect, was to
 204 ensure that our occupancy model was capable of correctly estimating the sign of the community-
 205 level logging parameter even when this effect is fairly small.

$$\text{Logit}(p_{i,j,k}) = \alpha_{i,k}^{detect} + \beta_{i,k}^{Hunt(detect)} \times \mu_j \quad \text{Eq. S3}$$

$$Y_{i,j,k,l} \sim \text{Binomial}(\psi_{i,j,k,l} * p_{i,j,k}, S_j)$$

206 The detection-level of the model (Eq. S3) included draws from the posterior distribution of the
 207 parameters for hunting effect ($\beta^{Hunt(detect)}$) and intercept (α^{detect}), but did not include a
 208 logging effect. This simplification reduced computation time and enabled us to focus on our key
 209 question of whether we could measure an effect of logging on occupancy.

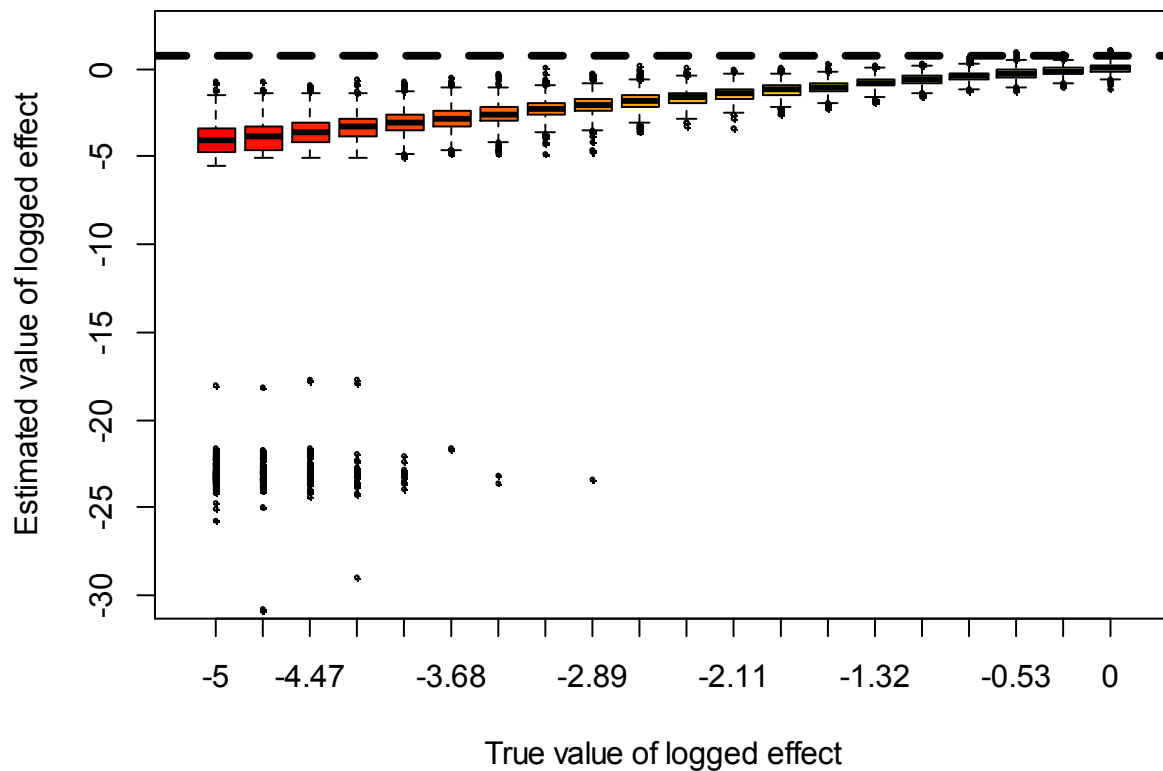
210 We simulated datasets for each of 1,074 posterior draws and the twenty values of
 211 community logging effect, for a total of 21,480 datasets. These simulations propagate uncertainty
 212 from our statistical estimation of effects as well as sampling uncertainty. To analyse these
 213 simulated datasets, we used a generalized linear mixed model (GLMM) approach in a frequentist
 214 framework, where we recorded $Y_{i,j,k,l}$ as a binary variable, with 1 representing any number of
 215 detection ≥ 1 , and 0 representing site and species combinations where no animals were observed.
 216 Species was included as a random intercept in the GLMM and logging was included as a fixed
 217 effect. Analysis of the simulated data with the GLMM enabled us to rapidly estimate parameters
 218 for a large number of models. In Table S1, we compare the parameter estimates from the GLMM
 219 for the intercept and logged-effect parameter to the community-level parameters for the intercept
 220 and logged-effect from the hierarchical occupancy model:

221 **Table S1.** Comparison of parameter estimates from the GLMM and the hierarchical occupancy
 222 model.

GLMM model			Hierarchical Occupancy model		
Parameter	Point estimate	95% CI	Parameter	Estimate (median of posterior distribution)	95% CI
Intercept	-2.03	-2.66 to -1.45	Community-level intercept	0.003	-1.01 to 1.02
Logging effect	0.75	0.39 to 1.12	Community-level logging effect	0.37	-0.72 to 1.57

223 As Table S1 shows, although the intercept parameters were fairly different (as expected from the
 224 different model frameworks), the logging effect estimated by the two different models was
 225 qualitatively similar.

226 Using the GLMM described above, we estimated the logging-effect for all 21,480
 227 datasets. We discarded models with convergence issues, leading to a total of 19,681 models. We
 228 found that the parameter estimates from the GLMM reasonably estimated the true parameters
 229 (Fig. S1), with a correlation of 57% between estimates and true values (Pearson's product-
 230 moment correlation). The largest estimation errors occurred when the true value of logging effect
 231 was moderately to strongly negative (< -3), in which case, there was a chance of overestimating
 232 the magnitude of this effect.



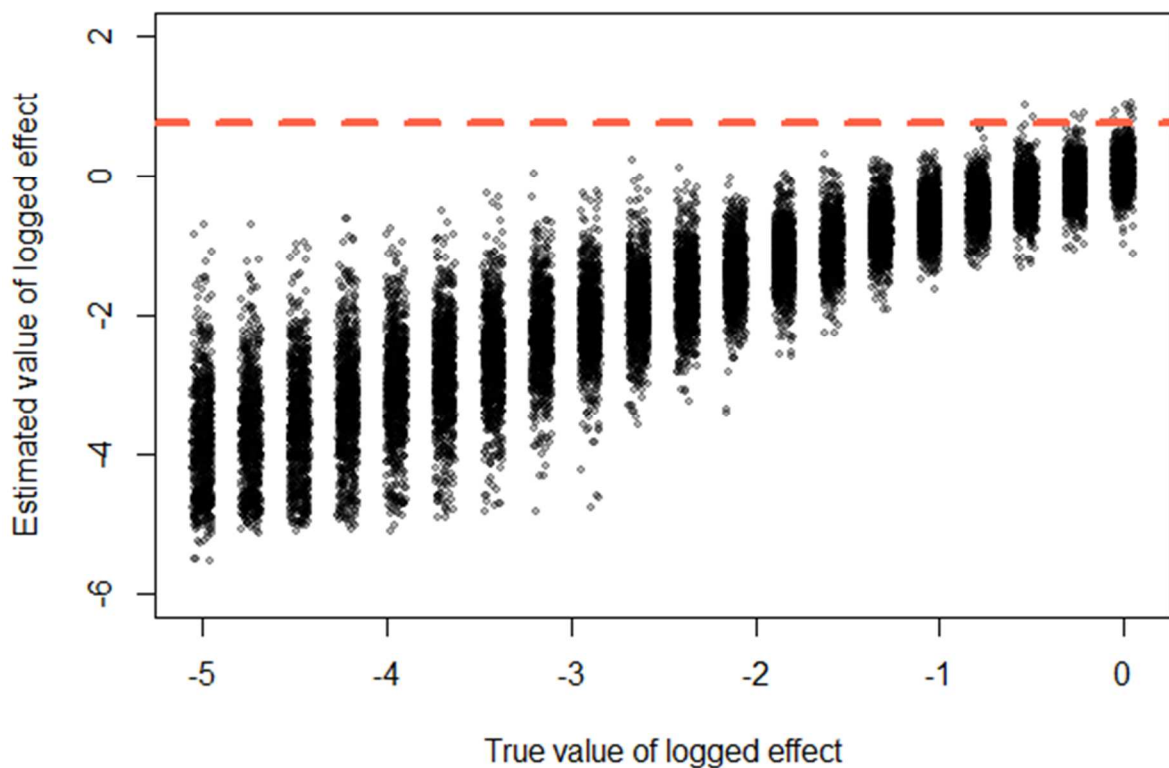
233

234 **Figure S1.** Parameter estimates from the GLMM compared to the true effect size for logging
 235 across our simulated datasets. The broken horizontal line indicates the estimated value of logging
 236 effect from the real data. The upper and lower edges of the box plots represent first and third
 237 quartiles, the thick black line within each box represents the median value, 'whiskers' represent
 238 minimum and maximum observations within 1.5 times of the upper and lower quartiles, and dots
 239 represents outliers.

240 Out of the 19,681 GLMM models, 1,212 incorrectly estimated the effect of community-
 241 level logging as positive whereas 3,844 estimated a non-significant effect of logging at a level of

1
2
3 242 $\alpha=0.05$. Most importantly, only 14 out of 19,681 models estimated the community level-effect of
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5
6 243 logging to be greater than the observed level of 0.75 (Fig. S2).
7
8

9 244 Overall, results from our power analysis suggest that we have sufficient statistical power,
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11 245 given our occupancy and detection rates and sample size, to capture a negative effect of logging
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14 246 on wildlife occupancy if it existed in our observations.
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247
248 **Figure S2.** Model estimates for the simulated datasets relative to our result from the hierarchical
249 model (broken red line). A single dot in this figure represents one simulated dataset. To better
250 visualize the 14 estimated values that were larger than our observed values, we truncated
251 extreme outliers in estimated values from this plot (entire range visible in Figure S1).