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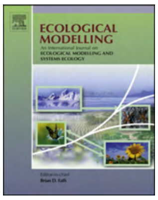

Modeling the impacts of hunting on the population dynamics of red howler monkeys (*Alouatta seniculus*)

Ruscena Wiederholt[a,*], Eduardo Fernandez-Duque[b,c], Duane R. Diefenbach[d], Rasanayagam Rudran[e]

[a] *Ecology Intercollege Graduate Degree Program, Pennsylvania State University, University Park, PA 16802, USA*
[b] *Department of Anthropology, University of Pennsylvania, 3260 South Street, Philadelphia, PA 19104-6398, USA*
[c] *Centro de Ecología Aplicada del Litoral, Corrientes-Argentina 3400, Argentina*
[d] *U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, Pennsylvania State University, University Park, PA 16802, USA*
[e] *National Zoological Park, Smithsonian Institution, PO Box 37012, MRC 551, Washington, DC 20013-7012, USA*

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ABSTRACT

Overexploitation of wildlife populations occurs across the humid tropics and is a significant threat to the long-term survival of large-bodied primates. To investigate the impacts of hunting on primates and ways to mitigate them, we developed a spatially explicit, individual-based model for a landscape that included hunted and un-hunted areas. We used the large-bodied neotropical red howler monkey (*Alouatta seniculus*) as our case study species because its life history characteristics make it vulnerable to hunting. We modeled the influence of different rates of harvest and proportions of landscape dedicated to un-hunted reserves on population persistence, population size, social dynamics, and hunting yields of red howler monkeys. In most scenarios, the un-hunted populations maintained a constant density regardless of hunting pressure elsewhere, and allowed the overall population to persist. Therefore, the overall population was quite resilient to extinction; only in scenarios without any un-hunted areas did the population go extinct. However, the total and hunted populations did experience large declines over 100 years under moderate and high hunting pressure. In addition, when reserve area decreased, population losses and losses per unit area increased disproportionately. Furthermore, hunting disrupted the social structure of troops. The number of male turnovers and infanticides increased in hunted populations, while birth rates decreased and exacerbated population losses due to hunting. Finally, our results indicated that when more than 55% of the landscape was harvested at high (30%) rates, hunting yields, as measured by kilograms of biomass, were less than those obtained from moderate harvest rates. Additionally, hunting yields, expressed as the number of individuals hunted/year/km^2, increased in proximity to un-hunted areas, and suggested that dispersal from un-hunted areas may have contributed to hunting sustainability. These results indicate that un-hunted areas serve to enhance hunting yields, population size, and population persistence in hunted landscapes. Therefore, spatial regulation of hunting via a reserve system may be an effective management strategy for sustainable hunting, and we recommend it because it may also be more feasible to implement than harvest quotas or restrictions on season length.

1. Introduction

Hunting remains one of the greatest mortality factors for large-bodied mammals inhabiting tropical rainforests, and is one of the most widespread forms of resource extraction in Amazonia (Redford, 1992; Peres, 2000b, 2001). Furthermore, harvest rates have increased over the last several decades due to loss of forested habitat, human population growth, increased accessibility to forests, commercialization of hunting, and use of new hunting technologies (Milner-Gulland and Bennett, 2003). As a result, overharvesting has often extirpated or reduced densities of mammals around neotropical settlements, and on an ecosystem scale, can precipitate even more serious problems like trophic cascades and loss of ecosystem functions and services (Redford, 1992; Alvard, 1995, 2000; Bennett et al., 2000; Peres, 2000b; Borgerhoff Mulder and Coppolillo, 2005; Peres and Nascimento, 2006; Thoisy et al., 2009). Yet, hunting provides an important source of protein, calories, and essential nutrients for indigenous and rural people living in South American tropical rainforests (Redford, 1992). Therefore, national governments have tried to encourage sustainable wildlife harvests. Despite this effort, sustainable hunting of neotropical pri-

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[*] Corresponding author at: 423 Carpenter Building, University Park, PA 16802, USA. Tel.: +1 814 867 0017; fax: +1 814 863 1474.

E-mail addresses: rpw143@psu.edu (R. Wiederholt), eduardof@sas.upenn.edu (E. Fernandez-Duque), ddiefenbach@psu.edu (D.R. Diefenbach), rudran@msn.com (R. Rudran).

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mates may be hard to achieve because even low harvest rates and subsistence hunting by an increasing number of people can cause severe population declines; and hunting often interacts with other threats in neotropical habitats (Thoisy et al., 2009). Furthermore, primate hunting varies according to local factors, can be difficult to quantify, and its effects on population densities can be confounded by habitat heterogeneity and quality. Therefore, hunting's impacts on primate populations can be unclear (Peres, 1990, 1991, 2000a; Mittermeier, 1991; Redford, 1992; de Thoisy et al., 2005; Di Fiore and Campbell, 2007; Thoisy et al., 2009; Arroyo-Rodríguez and Dias, 2010), and difficult to monitor in the neotropics, making it a challenge to effectively regulate harvests (Robinson et al., 1999; Novaro et al., 2000; Peres, 2000b, 2001).

Overcoming the above challenge is important because as much as one third of all primate species are threatened with extinction (Chapman and Peres, 2001; Strier, 2007). Among neotropical primates, the majority of ateline species are listed as vulnerable, endangered, or critically endangered (IUCN, 2010). Atelines are particularly vulnerable to anthropogenic disturbances because they are large bodied (3–15 kg) and long-lived species with low reproductive rates (Di Fiore and Campbell, 2007; Thoisy et al., 2009). Declines in their abundance have the potential to trigger significant changes in forest ecology. An estimated 80% of tree and shrub species in tropical wet forests rely on frugivorous animals for seed dispersal, and atelines are dispersers for many plant species (Levey et al., 1994; Julliot, 1996; Link and Di Fiore, 2006). Comparisons of hunted and un-hunted sites suggest changes in ateline abundance and distribution could alter seed dispersal patterns, and consequently, plant species composition and distribution in tropical forests (Wright et al., 2000; Nunez-Iturri et al., 2008; Brodie et al., 2009; Holbrook and Loiselle, 2009). The role of atelines in tropical forest conservation and the endangered status of numerous primates underscore the importance of developing an effective strategy for their conservation and long-term sustainable management.

A strategy proposed by several empirical studies suggests that in order to sustain harvestable mammalian populations it is important to maintain refugia, areas where hunting does not occur (Knowlton, 1972b; Novaro, 1995; Hill and Padwe, 2000; Novaro et al., 2000; Peres, 2001). However, these studies did not consider the dynamics of populations in a spatial context. Modeling studies also have estimated hunting sustainability but they used traditional wildlife management ideas (e.g. maximum sustainable yield) and assumed that harvests are spatially uniform (Caughley, 1977; Robinson and Redford, 1991; Robinson, 2000). Studies with non-uniform spatial harvests have shown that protecting a harvestable resource in part of its range would garner maximum sustainable yields (Joshi and Gadgil, 1991; McCullough, 1996), whereas other research indicate that source populations and size and shape of hunted areas are important for sustainable hunting and population persistence (McCullough, 1996; Gaona et al., 1998; Salas and Kim, 2002). However, such models are theoretical, rely on estimates of maximum rates of increase to provide indications of minimum reserve area (Joshi and Gadgil, 1991; McCullough, 1996), are specific for ungulates or felids (Gaona et al., 1998; Salas and Kim, 2002), and do not account for complex life histories and potential disruptions to a species' social structure from hunting.

Keeping the above issues in mind, we developed a spatially explicit model to examine the influence of hunting and un-hunted reserves on population persistence and hunting sustainability. The amount of reserve area in a landscape was of particular interest because the influence of refugia is an important conservation issue; albeit one that may be difficult to test empirically. Nonetheless, in hunted and disturbed landscapes, reserve areas promise to be a useful conservation strategy that merits further investigation.

For our spatially explicit model, we used an individual-based framework because it can incorporate individual variations, complex life histories, and dynamics commonly found on a local scale among social animals (Grimm and Railsback, 2005). Only a few spatially explicit, individual-based models have investigated the role of reserve areas on hunting sustainability (Salas and Kim, 2002), or hunting's influence on social structure and dynamics (Kenney et al., 1995; Whitman et al., 2004, 2007). Nevertheless, these effects could be particularly important for the sustainable management of a social species like the red howler monkey (*Alouatta seniculus*), a large bodied (4–11 kg.), long-lived (>22 years), polygynous primate (Eisenberg and Redford, 1999), which exhibits behaviors such as male–male reproductive competition, infanticide, and turnover of troop males that could make the species vulnerable to human hunting.

2. Site description

We parameterized our model using primarily a 30-year data set collected from a Venezuelan red howler population (Neville, 1972; Rudran and Fernandez-Duque, 2003) between 1969 and 1999 at Hato Masaguaral, a wildlife preserve and cattle ranch, in the Guárico State of Venezuela (8°34′N, 67°35′W). The ranch contains two major habitat types consisting of a continuous gallery forest found along the Guárico river, and a tropical savanna composed of matas, or forest patches, surrounded by seasonally inundated grassland (Troth, 1979). Annual rainfall is seasonal with a wet season from May to October and a dry season from November to April (Crockett and Rudran, 1987). The vegetation is semi-deciduous with many species of trees and shrubs losing their leaves in the late dry season. The elevation is approximately 70 m ASL, and average monthly temperatures vary from a minimum of 19–22 °C during the wet season to a maximum of 33–38 °C during the dry season (Troth, 1979).

3. Model description

3.1. The model's purpose

The purpose of constructing a spatially explicit, individual-based model was to incorporate the life history traits and troop dynamics of *A. seniculus* adequately so we could examine the effects of hunting and un-hunted reserves on population dynamics and the options for sustainable hunting. We conducted simulations using NetLogo, an individual-based modeling program (Center for Connected Learning and Computer-Based Modeling, Northwestern University, version 4.0.2, 1999).

3.2. Variables and scales

We created a model that included a 101 × 101 grid representing a 20.2 km × 20.2 km landscape (408 km^2) with hunted and un-hunted areas. We assumed a uniform habitat, and to simulate empirical evidence that the majority of hunting in the neotropics occurs around permanent settlements (Hames, 1980; Alvard et al., 1997; Novaro et al., 2000; Koster, 2007), our model used circular hunted areas of 5 km radius. Harvest rates within these areas were also based on reported indigenous neotropical hunting patterns and varied with distance from the center of the hunted patch (Hames, 1980; Koster, 2007). Starting at the center of the patch and moving to the edge, harvest rates within rings encompassing 1/5 of the patch radius were set at 35%, 100%, 84%, 93%, and 58%, respectively of the overall model's harvest rate. If there were one or two hunted patches in the landscape, they were placed randomly, and if there were three, four, or five hunted patches, they were placed equidistant from each other. If there were five patches, the outer rings of different patches overlapped by 9% of their area, but in all other cases hunted patches were completely surrounded by reserve area. Harvest rates, which remained constant over time, corresponded to hunter effort and represented the probability of hunting mortality for howler monkeys. An individual's chance of being hunted depended on its location within a hunted patch, its age class, and the model's overall harvest rate. The carrying capacity of the habitat (44.8 individuals/km^2) was based on the mean density of eleven red howler populations (Chapman and Balcomb, 1998). For the estimation of density-dependent survival rates, the model assumed that individuals could only detect conspecifics that were within 1 km of themselves. This distance, which corresponds to the mean maximum day range (Di Fiore and Campbell, 2007), is used as an approximation of the number of conspecifics with which an individual would be interacting and competing most frequently. We incorporated different sex and age classes (adults, subadults, juveniles, and infants) of red howler monkeys in the model in proportion to the age distribution of the undisturbed population that contributed the 30-year data set (Rudran and Fernandez-Duque, 2003). We classified juvenile sizes into large, medium, and small categories for males and large and small categories for females. For each scenario, we ran the model with annual time steps for 100 years.

3.3. Overview of processes

In each time step, individuals of the model population underwent the six life history processes given below (see Appendix A for a complete description of processes).

1. Adults aged 1 year, whereas immature individuals advanced to the next age class.
2. Natural mortality, which varied according to the age and sex of the individual, could occur.
3. Adults of both sexes reproduced. Females whose infants experienced infanticide in the previous time step had a greater likelihood of reproducing than females whose infants did not experience an infanticidal event.
4. Troops changed social status. Bisexual extra-troop associations, consisting of dispersing individuals, could become established troops if they produced an infant.
5. Individuals of both sexes dispersed and searched for suitable troops or associations to join. Adult and subadult males could also enter troops in this process, which could result in infanticides and the death or eviction of the resident and invading males.
6. Hunting occurred in hunted areas. Our model reflected indigenous hunting patterns by placing the majority of hunting pressure on older individuals, but it did not include a hunting bias between the sexes. Nevertheless, more adult females than adult males were hunted because they comprised a larger segment of the population (see Appendix A for a complete list of the model input parameters).

3.4. Design concepts

Emergence: Several model outcomes emerged from individual traits and behaviors: birth rates were density-independent, whereas survival rates were density-dependent which produced logistic growth in the population. In addition, patterns of population loss, hunting yields, and social dynamics emerged under various hunting scenarios that were not imposed by the model structure.

Collectives: Individuals belonged to troops, and only one troop could occur in a cell (representing an area of 0.04 km^2), which corresponds to a minimum home range estimate for *A. seniculus* (Crockett and Eisenberg, 1987).

Sensing and fitness: Individuals of both sexes could assess troop characteristics (including their status and composition), but did not recognize differences between hunted and un-hunted areas. They also sought to improve their fitness by dispersing from large troops where reproductive opportunities may have been limited. Dispersing males associated with dispersing females and tried to establish new troops or attempted to take over the established troops they encountered.

Interactions: Individuals interacted during reproduction, turnovers, and dispersal (i.e. during eviction from or entry into troops and during new troop formation).

Stochasticity: We incorporated stochastic processes into birth, dispersal, survival, turnovers, and hunting rates. For stochastic functions, the model generated a uniform (0, 1) random number, and if it was less than the specified probability of the process, the action occurred. We also included logical rules in the processes of dispersal and reproduction to account for troop composition and females' past reproductive history.

3.5. Initialization

We created the initial population's sex-age structure in proportion to the mean age and sex distribution of the undisturbed population that contributed the 30-year data set (Rudran and Fernandez-Duque, 2003). The initial population density was at carrying capacity. The model grouped individuals into unimale or multimale troops, with initial multimale troops having two or three adult males. Approximately 46% of the initial troops were multimale and 54% unimale, which corresponded to the mean composition of the undisturbed population. Initial multimale and unimale troops varied in size from four to 18 and from three to 18 individuals, respectively. The distribution of individuals among sex and age classes within troops varied and there were $\leq$18 individuals and $\leq$4 adult females per troop (Rudran and Fernandez-Duque, 2003). The model grouped some immature individuals of an appropriate age into bisexual associations (non-established troops consisting of dispersing individuals). Each troop was placed in a randomly selected cell (without replacement) within the hunted or un-hunted areas.

We used the 30-year data set to estimate fecundity, survival, and dispersal rates, and to obtain information on the mean age distribution, sex ratio at birth, troop composition, and howler lifespan (see Appendix A for a complete list of the model input parameters). We estimated mean birth rates from the inter-birth intervals of 556 infants born to 124 females in the population. Using a known fate analysis, we estimated maximum and minimum annual survival and dispersal rates based on a 9-year portion of the long-term dataset. We obtained information from the literature on the possible causes of dispersal, dispersal distance, extra-troop associations, new troop formation, likelihood of male turnovers and infanticides, and factors governing turnover success (Rudran, 1979; Sekulic, 1983; Crockett, 1984; Crockett and Sekulic, 1984; Agoramoorthy and Rudran, 1993; Crockett and Pope, 1993).

4. Sensitivity analyses and simulation experiments

We measured the sensitivity of our model to variation in the input parameters. For each analysis, we recorded the following output parameters: end and average population size, mean annual growth rate, population persistence, and mean number of turnovers, births, and infanticides per year. We altered ten input parameters which we hypothesized would strongly influence population growth, or for which estimates in the literature were either

Table 1
Model input parameters altered in the sensitivity analysis. Parameters were tested at their maximum or minimum values (when a range of estimates was available), or plus or minus 50% of their values in the model (when few estimates were available). An extreme parameter value was also tested in two cases.

Parameter probabilities	Baseline values	Sensitivity analysis (min value, max value, extreme value)
Reproduction with surviving infant	0.35	0.17, 0.57
Reproduction after infanticide	0.42	0.19, 0.78
Turnover success	0.12	0.06, 0.17
Male death during turnovers	0.002	0.001, 0.004, 0.01
Infanticide	0.50	0.45, 0.56
Ability of 1 invading male to evict or kill resident males	0.25	0.13, 0.38
Ability of 2 invading males to evict or kill resident males	1.00	0.50, 1.00
Invading males join troop or are evicted from troop after unsuccessful turnover	0.50	0.25, 0.75
Adult female survival	0.90	0.75, 0.95, 0.59
Subadult female survival	0.81	0.53, 0.89
Juvenile female survival	0.87	0.64, 0.93
Infant female survival	0.92	0.67, 0.94

lacking or based on studies with small sample sizes (Table 1). We assessed the model's sensitivity to the maximum and minimum values of a parameter when a range of estimates was available. If few empirical estimates were available, we assessed model sensitivity by varying parameters by ±50% of the best estimate. We also conducted a control run using the best estimates for each parameter. For each sensitivity analysis and the control run, we ran the model for 100 time steps (years) for 100 iterations.

The model's output included the total population size, population sizes in the hunted and un-hunted areas, population persistence, mean annual population growth rate, total number of individuals hunted, location of hunting, biomass hunted, and the number of turnovers, births, infanticides, and male deaths that occurred during turnovers. We calculated the total biomass hunted using the mean weights of the different sex and age classes (Thorington et al., 1979; Di Fiore and Campbell, 2007). We measured population sizes as both the size after 100 years (end population size) and mean size during the 100 years (average population size). For technical reasons related to the simulation software, population extinction was assumed to have occurred when population size declined to <1% of carrying capacity.

To elucidate the effects of hunting on population dynamics we used three different rates of harvest and five different sizes of hunted areas in our model. Preliminary analyses indicated that annual harvest rates of 1%, 5%, and 30% of the population corresponded to light, moderate, and heavy hunting intensities. Thus, we ran each model with a light (1%), moderate (5%), and heavy (30%) harvest rate for simulations with 18%, 55%, 74%, 83%, and 100% of the landscape in hunted areas. The first four simulations represented 1, 3, 4 and 5, hunted patches, respectively in the landscape. We also ran a simulation with a moderate harvest rate and 2 hunted patches (37%) in the landscape. For each scenario, we ran the model for 100 time steps (years) and 500 iterations.

5. Results

5.1. Sensitivity analyses

The model was robust to variations in parameter values as shown by the sensitivity analyses (Fig. 1). The mean population growth rate varied little from the control run of the model for the majority of parameters (<2% difference from the control run's value, Fig. 1a). Still, lower values of adult female reproduction and survival reduced the mean population growth rate by as much as 14.7% from the control run's value. Similarly, average population size was also significantly altered when rates of female survival, reproduction, or male survival during turnovers were varied (as much as a 81% difference from the control run's population size), whereas variations in other parameters resulted in only moderate changes to population size (<9% difference from the control run's population size, Fig. 1b).

5.2. Population dynamics and population persistence

The populations were quite resilient to extinction, and in all but one scenario persisted for 100 years (Fig. 2a). The only case of population extinction (i.e. a population decline to <1% of car-

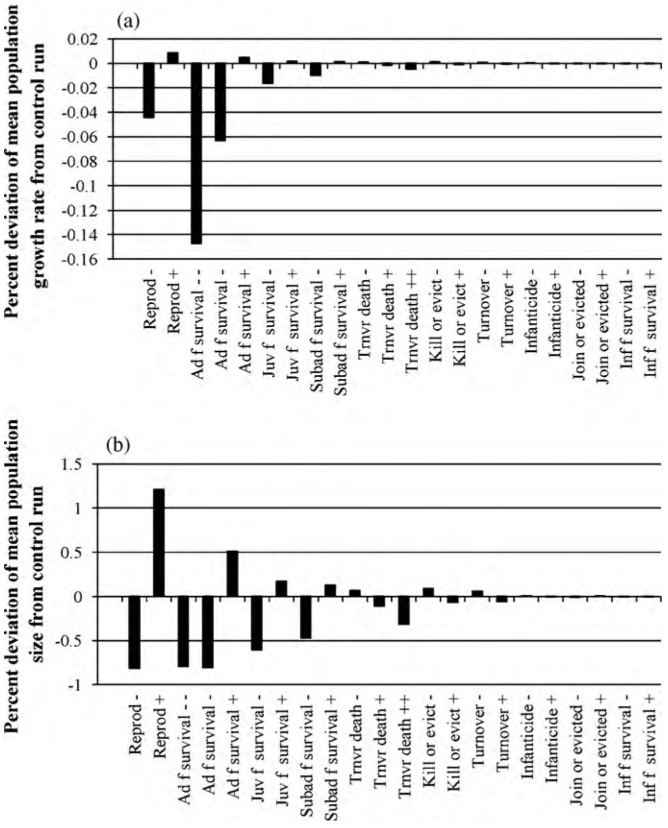

Fig. 1. Sensitivity analyses results for (a) mean population growth rate (b) and mean population size over 100 years expressed as percent deviation from the control run's value. Each altered input parameter was run for 100 iterations, + or − signs indicate positive or negative alterations from the base model's values. Codes are as follows: Reprod = probability of reproduction; Ad f survival = adult female survival probability; Juv f survival = juvenile female survival probability; Subad f survival = subadult female survival probability; Trnvr death = probability of male death during turnovers; Kill or evict = probability of invading males being able to either evict or kill resident males; Turnover = turnover probability; Infanticide = probability of infanticide; Join or evicted = probability of unsuccessful invading males being evicted or joining the troop; Inf f survival = infant female survival probability.

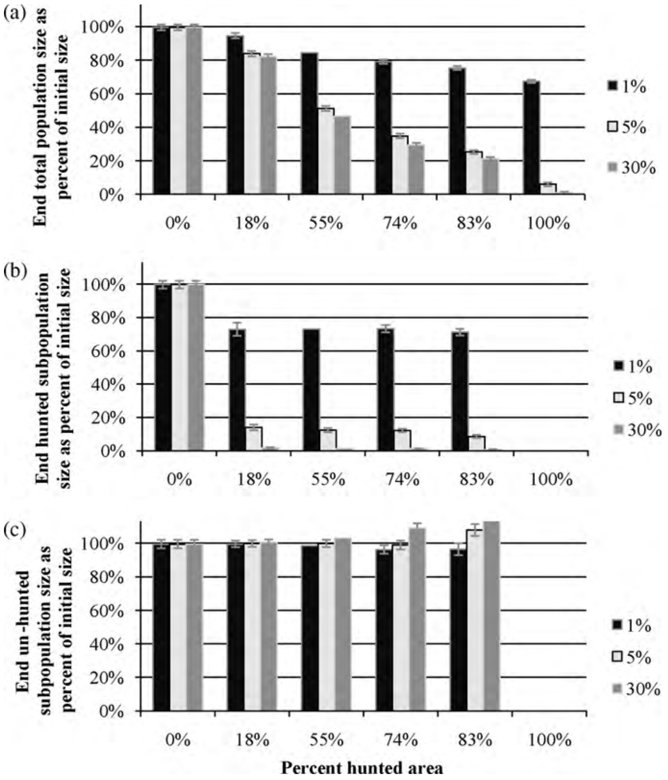

Fig. 2. End population sizes as percent of initial population sizes for (a) the total population, (b) hunted subpopulation, (c) and un-hunted subpopulation at the various harvest rates (1%, 5%, and 30%) after 100 time steps (years). Error bars show ±1 s.d.

rying capacity) occurred when the entire landscape was hunted at high (30%) harvest rates (Fig. 2a). In this scenario, populations went extinct, on average, in 13.8 years (s.d. = 0.7). In all other scenarios, populations persisted despite, in some cases, quite large reductions in total size. For instance, light (1%) harvest rates reduced the total end population size after 100 steps (years) between 5% and 33%, and moderate (5%) harvest rates reduced it between 16% and 94% (Fig. 2a). These declines in total population size were the result of large losses in the hunted subpopulation, which is reflected by the fact that moderate (5%) harvest rates reduced the hunted subpopulation size by 86–91%, while high (30%) harvest rates reduced it by >98% (Fig. 2b). In contrast, the size of the un-hunted population remained relatively constant when the hunted area and harvest rate increased elsewhere (Fig. 2c); and it was the stability of the un-hunted subpopulation that allowed the total population to persist despite large losses, and avoid overall population extirpation.

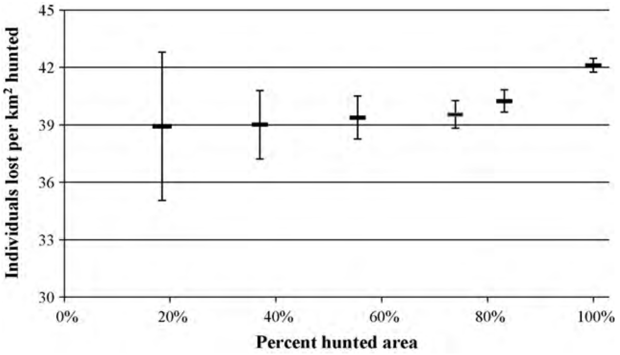

Fig. 3. Total population losses after 100 years, expressed as individuals lost per km^2 hunted, for various amounts of hunted area at a 5% harvest rate. Error bars show ±1 s.d.

Increasing the area hunted within a landscape also caused larger proportional declines in the hunted subpopulation and total population (Figs. 2 and 3Figs. 2b and 3). To compare the different models, we standardized the decline in overall population size as number of individuals lost per km^2 of area hunted. When the hunted area increased at a moderate (5%) harvest rate, the decline per unit area of the total population increased from 38.9 to 42.1 individuals lost per km^2 hunted (Fig. 3). In addition, at a moderate (5%) harvest rate, the proportional decline of the hunted subpopulation was greater as the amount of hunted area increased. For instance, declines of hunted subpopulations in landscapes with 83% hunted area were 5.3% greater than in landscapes with 18% hunted area (Fig. 2b). Furthermore, in models where 55% or more of the landscape was hunted at a high (30%) rate or 83% was hunted at a moderate (5%)

Table 2
Effects of hunted area and harvest rate on demographic parameters expressed as mean annual rates.

Hunted area (%)	Harvest rate (%)	Number of infanticides/1000 ind. ± 1 s.d.	Number of births/1000 ind. ± 1 s.d.	Number of turnovers/1000 ind. ± 1 s.d.	Male deaths per turnover ± 1 s.d.	Total turnover deaths/1000 ind. ± 1 s.d.[a]
Control	0	3.4 ± 0.1	145.2 ± 1.6	16.6 ± 0.1	0.4 ± 0.0	10.4 ± 0.1
18	5	3.4 ± 0.1	144.7 ± 1.8	16.8 ± 0.1	0.4 ± 0.0	9.7 ± 0.2
37	5	3.5 ± 0.1	144.1 ± 2.0	17.2 ± 0.2	0.3 ± 0.0	9.0 ± 0.2
55	5	3.5 ± 0.1	143.3 ± 2.3	17.7 ± 0.2	0.3 ± 0.0	8.4 ± 0.2
74	5	3.6 ± 0.1	142.1 ± 2.8	18.6 ± 0.3	0.2 ± 0.0	7.9 ± 0.2
83	5	3.6 ± 0.1	141.8 ± 3.1	19.0 ± 0.4	0.2 ± 0.0	7.6 ± 0.2
100	5	3.8 ± 0.2	139.0 ± 4.0	21.4 ± 0.5	0.2 ± 0.0	8.0 ± 0.3
18	1	3.4 ± 0.1	145.0 ± 1.7	16.8 ± 0.1	0.4 ± 0.0	10.3 ± 0.2
18	5	3.4 ± 0.1	144.7 ± 1.8	16.8 ± 0.1	0.4 ± 0.0	9.7 ± 0.2
18	30	3.4 ± 0.1	145.0 ± 1.9	16.6 ± 0.1	0.4 ± 0.0	9.3 ± 0.2
55	1	3.5 ± 0.1	144.6 ± 1.9	17.4 ± 0.2	0.4 ± 0.0	10.1 ± 0.2
55	5	3.5 ± 0.1	143.3 ± 2.3	17.7 ± 0.2	0.3 ± 0.0	8.4 ± 0.2
55	30	3.4 ± 0.1	144.9 ± 2.4	16.7 ± 0.2	0.2 ± 0.0	7.3 ± 0.2
74	1	3.6 ± 0.1	144.4 ± 2.0	17.7 ± 0.2	0.4 ± 0.0	10.0 ± 0.2
74	5	3.6 ± 0.1	142.1 ± 2.8	18.6 ± 0.3	0.2 ± 0.0	7.9 ± 0.2
74	30	3.4 ± 0.1	145.1 ± 3.3	16.9 ± 0.3	0.2 ± 0.0	6.4 ± 0.2
83	1	3.6 ± 0.1	144.2 ± 2.1	18.0 ± 0.2	0.3 ± 0.0	9.9 ± 0.2
83	5	3.6 ± 0.1	141.8 ± 3.1	19.0 ± 0.4	0.2 ± 0.0	7.6 ± 0.2
83	30	3.5 ± 0.1	145.9 ± 3.5	17.2 ± 0.3	0.2 ± 0.0	6.2 ± 0.2
100	1	3.7 ± 0.1	143.8 ± 2.4	18.4 ± 0.2	0.3 ± 0.0	9.7 ± 0.2
100	5	3.8 ± 0.2	139.0 ± 3.9	21.4 ± 0.5	0.2 ± 0.0	8.0 ± 0.3
100	30	4.1 ± 0.4	124.2 ± 5.2	39.3 ± 2.1	0.3 ± 0.0	17.7 ± 1.3

[a] Male deaths and infanticides due to turnovers.

Table 3
Changes in hunting yields for different harvest rates and amounts of hunted area.

Hunted area (%)	Harvest rate (%)	Mean annual biomass hunted (kg) ± 1 s.d.	Mean annual biomass hunted (kg)/percent hunted area
18	5	203.2 ± 7.3	11.0
37	5	399.7 ± 11.4	10.8
55	5	583.8 ± 12.5	10.5
74	5	770 ± 16	10.4
83	5	804.6 ± 17.7	9.7
100	5	889.4 ± 17.4	8.9
18	1	108.7 ± 3.5	5.9
18	5	203.2 ± 7.3	11.0
18	30	230.8 ± 5.3	12.5
55	1	326 ± 5.8	5.9
55	5	583.8 ± 12.5	10.5
55	30	600.9 ± 10.2	10.8
74	1	435.6 ± 6.9	5.9
74	5	770 ± 16	10.4
74	30	759.3 ± 12.2	10.3
83	1	503.3 ± 7.8	6.1
83	5	804.6 ± 17.8	9.7
83	30	724.3 ± 9.5	8.7
100	1	638.7 ± 9.5	6.4
100	5	889.4 ± 17.4	8.9
100	30	5054.2 ± 2.5	50.5

rate, the un-hunted population actually increased beyond its initial value (Fig. 2c).

5.3. Demographic parameters

Increasing the harvest rate or hunted area caused declines in the number of male deaths per turnover and in the total turnover-related deaths per 1000 individuals (Table 2). For instance, when harvest rates increased from 1% to 30% in a landscape with 83% hunted area, turnover parameters dropped from 0.35 to 0.16 and 9.9 to 6.2 for male and total turnover-related deaths, respectively. The number of births, infanticides, or turnovers did not exhibit clear trends when the harvest rate increased, but they did undergo changes when the area hunted increased. For example, when the area hunted at a moderate (5%) rate increased from 18% to 100%, the annual number of infanticides per 1000 individuals increased slightly (from 3.4 to 3.8) along with turnovers per 1000 individuals (from 16.8 to 21.4). Under the same scenario, the annual number of births per 1000 individuals declined (from 144.7 to 139). Thus, when the hunted area increased, reproduction and infant survival declined while the number of turnovers increased.

Demographic parameters exhibited the greatest changes when the entire landscape was hunted at a high (30%) rate (Table 2). As harvest rates increased from 1% to 30%, the number of infanticides increased from 3.7 to 4.1 and the number of births decreased from 143.8 to 124.2. The number of turnovers and turnover-related deaths also increased sharply from 18.4 to 39.3 and from 9.7 to 17.7, respectively.

5.4. Hunting yields

Hunting yields, expressed as mean annual biomass (kg) obtained from all hunted areas, increased when hunting was maintained at low (1%) or moderate (5%) rates while increasing the proportion of the hunted area (Table 3). For instance, at a moderate (5%) harvest rate, hunting yields increased from 203 kg to nearly 890 kg as the hunted area increased from 18% to 100%, and each additional percent of the landscape hunted translated into a mean gain of 10.2 kg of biomass hunted/year (Table 3). However, at a 5% harvest rate, the yield per unit area hunted declined as the size of the hunted area increased; thus, the additional gain from hunting larger areas declined with reduced reserve area. Furthermore, when harvest rates increased, annual yields varied according to the amount of reserve area in the landscape. If 55% or less of the landscape was hunted, annual yields increased with higher harvest rates. However, when more than 55% of the landscape was hunted at high (30%) rates, annual yields were less than those obtained at moderate (5%) harvest rates. When the entire landscape was hunted at a high (30%) rate, the annual yield was very high. However, because the population was extirpated quickly (on average within 14 years), the total yield (69,838.9 kg) over 100 years was less than the total yield obtained at a moderate harvest rate (88,944.4 kg) over the same period.

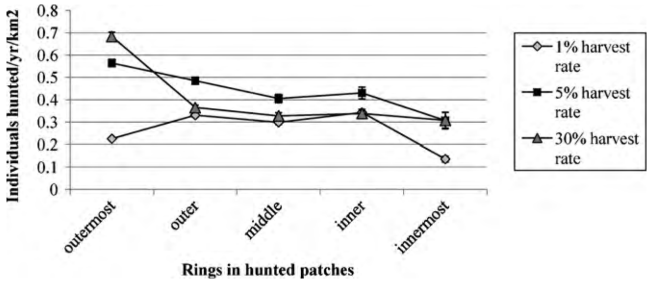

Fig. 4. Hunting yields (individuals/year/km^2) obtained in different rings of the hunted patches for various harvest rates with 74% hunted area. Error bars show ±1 s.d.

Hunting yields, expressed as the number of individuals hunted/year/km^2, varied according to harvest rate and the location of hunting (Fig. 4). For instance, at a low (1%) harvest rate in a landscape with 74% hunted area, the yields obtained in the different rings of a hunted patch followed the pattern set by the model's hunting rates, i.e., they were greater in the three middle rings than in the inner- and outer-most rings (Fig. 4). However, as harvest rates increased the outer-ring, which abutted un-hunted reserve areas, produced a greater yield than all other rings. This indicates that maintaining un-hunted reserves will increase hunting yields obtained at moderate and high harvest rates adjacent to these areas.

6. Discussion

6.1. Population dynamics and population persistence

Our results showed that harvest rates and size of reserves had important independent and synergistic effects on sustainable hunting and population persistence. In all scenarios where the landscape included any reserve areas, the population persisted for 100 years and hunting was sustainable; the population was extirpated only when the entire landscape was hunted at a high (30%) rate (Fig. 2a). The overall population's persistence was due to the stability of the un-hunted population, which maintained a relatively constant density in most scenarios (Fig. 2c). These findings are consistent with theoretical and experimental studies which concluded that if a certain minimum area was set aside as a reserve, the population would be protected from extinction (Salas and Kim, 2002; Chapron et al., 2003; Fryxell et al., 2006). Also, we found that population losses increased disproportionately when reserve area decreased (Figs. 2b and 3), indicating that landscapes containing larger reserves had greater capacities to mitigate the effects of hunting. These results support McCullough's (1996) finding that spatial control of hunting via the establishment of reserves was more effective than numerical control through hunting quotas at preventing overharvesting and population extirpation. However, while others estimated that a minimum of 65–100% reserve area was needed to ensure population viability (Joshi and Gadgil, 1991; Novaro et al., 2000), we found that red howlers could persist indefinitely in landscapes with smaller reserves. This difference may have been the result of others using a model that assumed complete mixing of hunted and un-hunted populations, which did not occur in our model. Therefore, reduced dispersal into hunted areas in our model may have allowed the population to persist in a landscape with smaller refugia.

Our results are congruent with Robinson and Redford's (1991) estimate that a maximum of 2.52 kg/km^2 can be harvested sustainably for *Alouatta* species. Assuming a uniform spatial harvest, when the harvest exceeded 2.52 kg/km^2 in our model the population was extirpated. Robinson (2000) estimated the maximum annual sustainable offtake of a population (expressed as the percent of the standing population or biomass) is 3% for *Alouatta* species. In our models, if the entire landscape was hunted at a 30% harvest rate the population was extirpated but not at a 5% harvest rate. This discrepancy arises from the fact that 5% was the model's overall harvest rate, but it was modified according to the actual location of hunting within the hunted area. In the majority of cases, the location of hunting lowered the harvest rate. Therefore, the percent of the population hunted did not exceed the 3% maximum sustainable offtake of the total population.

In our model, the reserve subpopulation actually increased beyond its initial value when hunting occurred at moderate or high rates over large areas (Fig. 2c). This unexpected increase was likely due to dispersing individuals moving into reserves from extensively hunted areas because of declining numbers, or remaining in un-hunted areas to improve their chances of joining a troop. Thus, the behavior of dispersing individuals would have exacerbated the population losses in extensively hunted areas. This explanation is consistent with findings of others who have noted limited dispersal into areas with suppressed population densities (Porter et al., 1991, 2004).

6.2. *Demographic parameters*

Although our model considered many aspects of red howler social structure, it may not have captured all aspects of the complex life history of this species. Despite these limitations, the model allowed us to explain several important demographic changes with respect to hunting and red howler social dynamics (Table 2). The decline of adult male deaths and total deaths (male deaths plus infant mortality) per turnover was most likely due to hunting mortality resulting in fewer males per troop. This would also reduce the likelihood that dispersing males would leave their troops with a partner, and therefore, single invading males would have been less capable of killing resident males during a turnover. In addition, the increases in the rate of turnovers and infanticides as hunted area increased were also probably due to hunting, which would have reduced the number of resident males per troop and increased the success rate of turnovers as well as infanticides (Table 2). The drop in birth rates observed under the same scenario likely reflected the hunters' preference to harvest the larger-bodied adult females rather than younger age classes, as prescribed by our model. Therefore, in our model of social dynamics, the effects of hunting extended beyond the number of individuals harvested, and led to the disruption of the social structure resulting from increased turnovers and infanticides and decreased reproduction and infant survival. These alterations in social structure could have had synergistic effects and may have added to population losses already caused by hunting.

6.3. *Hunting yields*

We found that in landscapes with large reserves the yield increased as harvest rates increased, but when hunted areas exceeded 55% of the landscape, yields declined at high harvest rates (Table 3). Our results are similar to those presented for tapirs, where an increase in the un-hunted subpopulation increased the maximum sustainable harvest rate of a hunted subpopulation (Salas and Kim, 2002). Hunting yields also increased in areas adjacent to reserves, suggesting that dispersal from un-hunted areas may help promote sustainable hunting (Fig. 4). Empirical observations of marine reserves in more than a dozen countries support this conclusion, and for a variety of species fishing effort was concentrated around reserve boundaries (Gell and Roberts, 2003). In most scenarios of our model, the circular hunted patches were completely surrounded by reserve area. This patch design should have maximized immigration rates into hunted patches and most likely sustained hunting yields as well. This is consistent with empirical studies that hypothesized nearby un-hunted areas permitted high rates of hunting (Hill and Padwe, 2000; Knowlton, 1972a,b; Novaro, 1995; Novaro et al., 2000; Peres, 2001). Although we did not explicitly examine other landscape geometries, different spatial configurations of hunted areas may have influenced hunting yields and population persistence.

6.4. *Reserves as a management tool*

Both empirical and modeling studies, including this one, have shown that reserves promote population persistence, and establishing them could help sustainable management of hunted populations (Knowlton, 1972a; Joshi and Gadgil, 1991; Novaro, 1995; McCullough, 1996; Gaona et al., 1998; Hill and Padwe, 2000; Novaro et al., 2000; Peres, 2001; Salas and Kim, 2002). In the neotropics, where monitoring and management capabilities are limited, reserves provide opportunities for spatial control of hunting, which could perhaps be more easily enforced than restrictions on hunting quotas (Novaro et al., 2000). Spatial control of hunting may also be desirable because continued increases in human populations and the easy accessibility of the Amazon basin are likely to make passive forms of reserve protection (through religious or social taboos, etc.) ineffective (Milner-Gulland and Bennett, 2003; Peres and Lake, 2003; Borgerhoff Mulder and Coppolillo, 2005; Diefenbach et al., 2005). Therefore, active management of reserve areas, with the help or direction of local communities becomes important to ensure sustainable primate populations (Borgerhoff Mulder and Coppolillo, 2005).

Our results indicated that even small reserve areas were sufficient to promote hunting sustainability and prevent population extirpation. However, modern-day realities like hunting and poaching can undermine the effectiveness of small reserves. Furthermore, our model did not consider environmental stochasticity, habitat heterogeneity, or other factors such as climate change, pollution, or habitat fragmentation and degradation which could affect primate population dynamics (Wiederholt and Post, 2010). Thus, reserves larger than those prescribed by our model may be essential to ensure population persistence.

6.5. Suggestions for future research

Our model simulated a naturally occurring hunting pattern that reflected high adult female mortality, but other patterns like preferential hunting of adult or subadult males could be examined to further elucidate the impacts of hunting on primate populations. In addition, changing the spatial configurations of the landscape could help determine if this factor has any effect on hunting sustainability and population viability. Modeling the simultaneous effects of multiple variables such as hunting, climate change, and habitat loss could also be useful in designing and implementing primate conservation strategies since such a study would effectively address the potential for several environmental variables to synergistically decrease population viability (Mora et al., 2007; Brook et al., 2008).

7. Conclusions

Due to hunter preference for large-bodied individuals, adult female red howler monkeys, which constituted the largest segment of the population, were most often the victims of hunting. Thus, hunting had the greatest negative impact on individuals that were essential for reproduction and population viability. Our results also showed that hunting disrupts troop social structure and increases rates of infanticides and turnovers while decreasing birth rates, which in turn exacerbates population declines due to hunting alone. Effective strategies for sustainable hunting are urgently needed because existing regulations based on restricting harvest quotas or season length are difficult to enforce. Spatial regulation of hunting via a reserve system may be easier to enforce, and our results indicated that appreciably high harvest rates were sustainable even with relatively small refugia. However, our models did not consider impacts other than hunting (e.g. climate change, habitat fragmentation) on primate populations, that may require larger reserve areas than our model recommends to ensure population viability.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.06.026.

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