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The Madingley general ecosystem model predicts bushmeat yields, species extinction rates and ecosystem-level impacts of bushmeat harvesting

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Traditional approaches to guiding decisions about harvesting bushmeat often employ single-species population dynamic models, which require species- and location-specific data, are missing ecological processes such as multi-trophic interactions, cannot represent multi-species harvesting and cannot predict the broader ecosystem impacts of harvesting. In order to explore an alternative approach to devising sustainable harvesting strategies, we employ the Madingley general ecosystem model, which can simulate ecosystem dynamics in response to multi-species harvesting given nothing other than location-specific climate data. We used the model to examine yield, extinctions and broader ecosystem impacts, for a range of harvesting intensities of duiker-sized endothermic herbivores. Duiker antelope (such as *Cephalophus callipygus* and *Cephalophus dorsalis*) are the most heavily hunted species in sub-Saharan Africa, contributing 34–95% of all bushmeat in the Congo Basin. Across a range of harvesting rates, the Madingley model gave estimates for optimal harvesting rate, and extinction rate, that were qualitatively and quantitatively similar to the estimates from conventional single-species Beverton–Holt model. Predicted yields were somewhat greater (around five times, on average) for the Madingley model than the Beverton–Holt, which is partly attributable to the fact that the Madingley simulates multi-species harvesting from an initially pristine ecosystem. Also, the Madingley model predicted a background local extinction probability for the target species of at least 10%. At medium and high levels of harvesting of duiker-sized herbivores, the Madingley model predicted statistically significant, but moderate, reductions in the densities of the targeted functional group; increases in small-bodied herbivores; decreases in large-bodied carnivores; and minimal ecosystem-level impacts overall. The results illustrate how general ecosystem models such as the Madingley model could potentially be used more widely to help estimate sustainable harvesting rates, bushmeat yields and broader ecosystem impacts across different locations and target species.

Keywords: bushmeat harvesting, Congo, ecosystem model, optimal, population dynamics

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Introduction

Present levels of wild animal harvesting are believed to be a major threat to survival for over half of the 178 species currently hunted in Central Africa (Abernethy et al. 2013). Bushmeat harvesting is an essential source of food and income for many poor rural communities in sub-Saharan Africa (Davies and Brown 2008, van Vliet et al. 2015, Van Vliet et al. 2017). Declining animal abundances and potential loss of species will detrimentally affect biological diversity and ecosystem integrity (Hooper et al. 2005, Abernethy et al. 2013), as well as the livelihoods and wellbeing of human population relying on meat from wild animals (or bushmeat) for cash income and additional protein (Njiforti 1996, Foerster et al. 2011, Golden et al. 2011, Nasi et al. 2011).

The standard approach to modelling the impacts of harvesting on a wild population is to use a population dynamic model, parameterised for the target species. A limitation is that single-species models are limited to studying the impacts of harvesting on that single species, and require species-specific or location-based data, and parameter estimates. By contrast, a practical approach to bushmeat harvesting over whole regions will require methods that can estimate the impacts of harvesting multiple species (Fa and Peres 2001), on both the target and the non-target species (Abernethy et al. 2013), over large regions where species- and location-specific data are sparse or not available (Fa and Brown 2009).

The modelling approaches currently used for assessing sustainability of bushmeat harvesting rely heavily on species monitoring data. These methods involve examining changes in animal abundances (Van Vliet et al. 2007) and harvest offtakes over time (Albrechtsen et al. 2007). Although declines in abundances of targeted species have been attributed to overharvesting in a number of Central African study sites (Fa et al. 2016), observational data is generally too limited (temporally, spatially) (Rodríguez et al. 2007, Fa and Brown 2009); though see Taylor et al. (2015) and/or too variable to reliably inform an effective management strategy (Gates 1996, Wilkie et al. 2001, Linder 2008).

Instead of relying on monitoring data of animal densities and offtakes, sustainability indices, such as Robinson and Redford's index (Robinson and Redford 1991) could be used to estimate sustainable harvest rates. The sustainability indices rely on point estimates of populations' carrying capacity and rate of population growth as inputs and are therefore less data intensive. This allows an estimation of sustainable levels of production of harvested populations (Wilkie and Carpenter 1999, van Vliet and Nasi 2008, Fa et al. 2014) which can then be compared with actual data on animal offtakes. Sustainable harvesting can also be defined in terms of probability of extinction of harvested species, where the threat of extinction must be kept below a maximum acceptable level (Mace and Lande 1991). However, to be effective most sustainability indices require accurate estimates of population parameters (Milner-Gulland and Akçakaya 2001, van Vliet and Nasi 2008, Weinbaum et al. 2013), such as the population carrying capacity and rate of population growth.

In practice, multiple species are targeted by hunters in tropical forests (Coad et al. 2019). A meta-analysis of 354 studies in sub-Saharan Africa revealed that a total of 318 species were reported as hunted (Ingram 2018), with ungulates, rodents and primates making up the majority of exploited species (Abernethy et al. 2013). To date, optimising harvesting beyond a single-species approach has been studied in theory (Bhattacharya and Begum 1996, Song and Chen 2001) and attempted in fisheries management (Yodzis 1994, Hutniczak 2015), where multi-trophic relationships are better described than in terrestrial ecosystems. Attempts to combine the understanding of multi-trophic interactions, current knowledge of biophysical systems (climate, nutrient flows, ecological processes) and how humans interact with the system (offtake levels, monitoring, socioeconomic drivers of demand) resulted in a number of ecosystem models, both global (Alkemade et al. 2009) and for separate biomes (Goodall 1975, Travers et al. 2007, Metzgar et al. 2013). With the exception of GLOBIO which has been extensively developed (Schipper et al. 2020) and used in a number of environmental outlook studies (Leclère et al. 2020), none of the terrestrial ecosystem models have been used for decision-making in practice due to their complexity. More recently, sophisticated end-to-end marine ecosystem models, such as Atlantis (Fulton et al. 2004, Fulton et al. 2011) and Ecopath with Ecosim (EwE) (Christensen and Walters 2004) have been developed and have now been applied to many marine ecosystems (for example, about 130 EwE models have been published) (Travers et al. 2007). However, deployment of these multi-species models requires extensive data inputs such as place-specific biological parameters (e.g. production rate, diet composition) and stock assessment survey data for a number of selected functional groups (Travers et al. 2007, Link et al. 2010). Consequently, these modelling frameworks cannot be applied without extensive parameterisation and good knowledge of the system (Link et al. 2010).

In terms of the effects of harvesting on ecosystem structure and functioning, a number of studies have reported increases in non-target species abundances (Peres and Dolman 2000, Linder 2008). In the Amazon, greater increases in abundances of large rodents and artiodactyls were reported in areas with higher levels of harvesting of arboreal monkeys, compared to moderately hunted areas (Bodmer et al. 1997). Peres (2000) showed that species resilience to harvesting correlated with body size (large-bodied species were more sensitive to persistent harvesting) in the Amazonian tropical forests. The secondary ecological effects of bushmeat harvesting should also be considered in assessing the sustainability of harvesting. For example, the important role of seed dispersers such as large monkeys and tapirs in the Brazilian Amazon (Brodie 2016), and of small and large primates in African lowland rainforests in carbon sequestration and forest regeneration (Effiom et al. 2013). However, bushmeat harvesting studies in tropical forests generally focus only on target species even though there is evidence that non-target species abundance also changes.

Thus, new methods are needed that deal with data scarcity while reflecting uncertainty, and that incorporate ecosystem and community impacts (Weinbaum et al. 2013). One potential solution is to employ an ecosystem model whereby fundamental ecological principles are used to simulate ecosystem structure and function, allowing emergent macroecological patterns to develop bottom–up. The Madingley general ecosystem model (hereafter referred to as the Madingley model) is such a model and has been tested against observations in a variety of virtual experiments (Harfoot et al. 2014, Bartlett et al. 2016, Newbold et al. 2020, Flores et al. 2019).

To date, the Madingley model (Purves et al. 2013, Harfoot et al. 2014) is the only such mechanistic ecosystem model that can be applied to any ecosystem type (marine and terrestrial), at any location and at minimum spatial resolution of 0.01° (organisms with body masses between 10 μg and 150 000 kg are simulated). It shares some important features with other ecosystem models such as aggregation of organisms into functional groups and the inclusion of biophysical drivers (climate, net primary production). However, unlike analogous models, the aggregation is not species-specific: it takes place on a functional level, based on traits such as diet (herbivore, carnivore, omnivore), metabolism (warm versus cold blooded) and adult and current body size, all of which are treated with well-established ecological relationships. Ecosystem dynamics (animal and plant) emerge in the Madingley model as a result of environmental inputs (such as air temperature and precipitation levels) working upon animals and plants, whose interactions between themselves and with the environment are based on fundamental concepts and processes derived from ecological theory, and defined at the scale of the individual organism. Importantly, all of these details mean that the model can simulate ecosystem dynamics at any location, without the need for explicit parameterisation by species or location. All that needs to be specified is the location (latitude, longitude) because this is needed to look up the climate drivers; and any perturbations made to the system. Crucially for this paper, these perturbations could include harvesting of any combination of plants and animals from the system.

On a functional group level, the Madingley model has been shown to provide robust approximations of the dynamics of animal populations (Harfoot et al. 2014). The model's outputs are spatially explicit and allow for the calculation of whole-ecosystem metrics such as animal abundance, body mass and trophic indices, which could all be used as indicators of systems' sensitivity to perturbations. To date, the Madingley model is the only model, to our knowledge, which allows exploration of such ecosystem-wide questions without specific and detailed parameterisation.

Here, we run a series of experiments in the Madingley model to explore the estimates it provides of sustainable bushmeat harvesting of duiker (*Cephalophinae*) from an African tropical rainforest. We chose this species and location for two reasons. First, duiker (*Cephalophinae*) is the most heavily hunted group in sub-Saharan Africa contributing 34–95% of all bushmeat captured in the Congo Basin (Wilkie and Carpenter 1999, Fa et al. 2005). Second, unlike many other hunted species, duikers have relatively good availability of species-specific ecological data such as density and reproduction rate estimates. These data allowed us to compare the Madingley model predictions to those of a single-species model for a well-studied species. A close match in predictions would tend to increase confidence in the use of the Madingley model for this purpose.

We examine the Madingley model predictions for duiker harvesting and compare them to predictions from single-species models. We also examine the Madingley model predictions for broader ecosystem impacts of harvesting, which cannot be done with the single-species models. We are interested in the model's estimates of sustainable harvesting in the tropical forest ecosystem, and the potential impacts of harvesting on ecosystem structure. We are ultimately interested in whether such an approach, using ecosystem modelling, could be developed to be useful in practice to assess harvest impacts on species worldwide including for species and locations which, unlike African duikers, have not been surveyed at all.

Material and methods

We begin by running the Madingley simulations for harvesting duiker *Cephalophus* spp. We create a Madingley model experiment that is as close as possible to those already run in Barychka et al. (2020) (summarised in the Supporting information) using the single-species model (Beverton–Holt) (Beverton and Holt 1957), to allow comparison of the outputs. The single-species model is parameterised using empirical estimates for Peters' duiker *C. callipygus* and bay duiker *C. dorsalis* (Feer 1988, Lahm 1993, Fa et al. 1995, Noss 1998a, b, 2000, Hart 2000, van Vliet and Nasi 2008), so qualitative and/or large quantitative differences between the models' outputs would increase our level of scepticism about using the Madingley model. On the other hand, a good level of correspondence between the models would increase our level of confidence in examining the Madingley predictions that the single-species model cannot make. We look closely at the yield, and the maximum harvest rate, for duikers as predicted by the Madingley model, including reporting on the uncertainty in the yields. This much was possible using the single-species model. However, we also examine the impact of duiker-like harvesting on the structure of the whole ecosystem, something that is only possible with the Madingley model. This allows us to assess whether and how apparently sustainable harvesting, could affect ecosystem structure.

Simulation protocol

The models

A schematic representation of the Madingley model (with harvesting) is given in Fig. 1, along with a representation of a single-species model (with harvesting). The Madingley model: receives environmental data based on user-defined latitude and longitude: location-specific empirical data on air temperature, precipitation levels, number of frost days, seasonality of primary productivity and soil water availability;

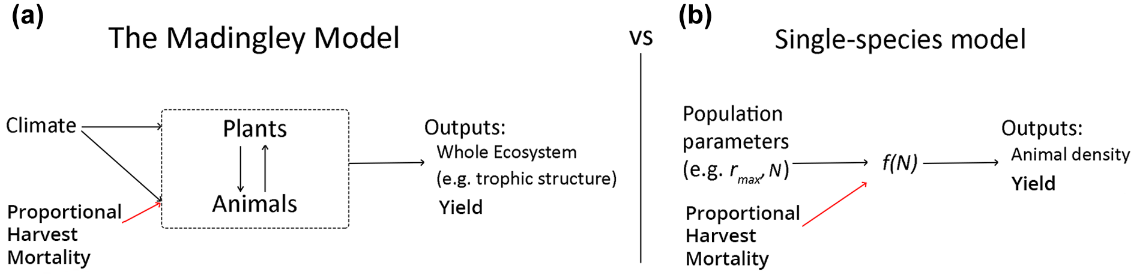

Figure 1. The Madingley model's inputs, modelled processes and outputs (a), compared to a single-species model's inputs, processes and outputs (b). Harvesting (here, constant proportional harvesting) is applied in both models. In (a) location-specific environmental data (e.g. air temperature, precipitation) are input into the model; plants and animals, that are initialised using a set of core functional relationships, exchange energy (eating, growth and reproduction, mortality); and a set of ecosystem characteristics (e.g. animal groups' densities) are output; in (b) estimates of population growth rates and carrying capacity are input and estimates of population densities are output.

simulates ecosystem dynamics from environmental inputs, and animal and plant dynamics described in the model using a set of core biological and ecological functional relationships (plant growth and mortality, and eating, metabolism, growth, reproduction, dispersal and mortality for animals); and outputs estimates of biological characteristics of the emergent ecosystem. We were particularly interested in animal abundances of the whole ecosystem (hunted and unhunted animal groups) and bushmeat yields. More details of the Madingley's processes and dynamics, and how these compare with a conventional single-species population dynamics model can be found in the Supporting information.

The Madingley model represents the state of the consumer (animal) part of the ecosystem in terms of the densities of individual animals with different functional traits. The densities change through time as individuals interact, in turn resulting in births, deaths, growth and dispersal, with the interactions (e.g. predation) defined entirely in terms of those traits. Although the model is defined by interactions among individuals, the simulation uses a computational approximation (based around so-called cohorts) to allow for all interactions among all individuals whose growth is simulated. The animal component of the ecosystem receives energy from the vegetation component, which growth is simulated using a simple stock and flow model, driven by climate, but affected by herbivory. For a detailed description see Harfoot et al. (2014).

As a comparison for the Madingley predictions, we used the Beverton–Holt population dynamics model (Beverton and Holt 1957) to represent single species responses to harvesting pressure (Barnes and Lahm 1997, Holden and Conrad 2015, Barychka et al. 2020):

$$N_{t+1} = \frac{r_t N_t}{1 + \left[\left(r_t - 1\right) / K\right] N_t} - \varphi N_t \qquad (1)$$

where N_t is the population density (individuals per unit area: in this case, animals km^{-2}) at time t; N_{t+1} is the population density in the following time step; K is the equilibrium population size in the absence of harvesting (carrying capacity); r_t is the density-independent intrinsic rate of natural increase (the balance of births and deaths) for year t; and φ is the harvest rate: the proportion of population targeted.

Environmental stochasticity (the year-to-year fluctuations in births and deaths) was represented by varying r_t between years, as described in Barychka et al. (2020) (also in the Supporting information).

We have not modelled stochastic variation in carrying capacity because we were not able to estimate the magnitude of variation to be supplied to the Beverton–Holt. Duiker-like target group densities in the Madingley differed from duiker carrying capacities as defined in the Beverton–Holt and, unlike the Beverton–Holt, population densities are emergent in the Madingley model and are not predefined. All Beverton–Holt simulations, data analysis and visualisations were carried out in R ver. 3.6.3 <www.r-project.org>.

Location

Our experimental site was simulated in the Madingley model on a 1° × 1° geographic grid cell (111.32 × 110.57 km) centred on 1°S, 15°E; the coordinates were selected to fall within the known duiker range in the tropical forests of the Republic of Congo. For the purposes of this study, no inter-cell migration was modelled, i.e. no animals were allowed from outside the experimental area.

Target group

The Madingley model is limited in its ability to track taxonomic identity of individuals: it simulates groups of animals characterised by a set of traits such as diet and current body mass (Supporting information). For reasons of computational efficiency, animal communities are represented by a collection of so-called cohorts, where individuals within the cohorts are treated as if they have fully identical traits. In locations with few species with similar traits, the Madingley predictions can be interpreted as predictions for the study species. However, in areas with higher biodiversity such as in this study, the model's predictions apply to an aggregate of species with similar traits. The model simulates multiple processes (death, reproduction, growth, dispersal); the individuals interact within communities (e.g. predation) and with their environment. This makes the model and its dynamics challenging to disentangle and understand. Despite this complexity, the model dynamics are relatively stable, and the predictions are relatively similar between runs. One of the reasons for this stability is the model's deterministic, rather than stochastic, form. Some uncertainty results from ordering of predator–prey events and from the model's random initial state (Supporting information), though it can be extended to incorporate more sources of uncertainty and stochasticity.

We simulated harvesting strategies for animals similar to duiker antelope (Table 1). We set up harvesting in the Madingley model to target terrestrial herbivorous endotherms, described using the following categorical traits: 'heterotroph – herbivore – terrestrial – mobile – iteroparous – endotherm'. This definition was further narrowed using two continuous traits: adult body mass and juvenile body mass (Lahm 1993, Noss 1998a). Under this definition, the target group for duiker-like harvesting included two out of the three most heavily hunted duiker species in Central Africa (Noss 1998a): Peters' duiker *Cephalophus callipygus* and bay duiker *Cephalophus dorsalis*. This excluded smaller-bodied herbivores (such as blue duiker *Cephalophus monticola*), but also other bushmeat species such as medium-sized herbivorous primates (such as *Piliocolobus badius*, mean weight = 7.75 kg, mean density = 156.3 animals km^{-2}) and large rodents (such as *Thryonomys swinderianus*, mean weight = 5.05 kg; mean density = 9.97 animals km^{-2}) (Fa et al. 2005).

Harvesting

In the Madingley model, a 1000-year 'burn-in' (no-harvesting) period was run (n = 30) to produce estimates of the ecosystem's equilibrium state in year 1000, including, for each functional group (carnivore/omnivore/herbivore): the number of surviving animal cohorts, abundances, biomass and adult body masses. These estimates of ecosystem's equilibrium ecological community were used as a starting point for subsequent harvesting simulations (i.e. the same 30 burn-in simulations were used as inputs for the subsequent harvesting simulations).

We used a constant proportional harvesting policy (Case 2000), where each year a proportion (harvest rate φ, Table 1) of animals were targeted. This harvest rate remained constant for the duration of harvesting period T (set at 30 years based on examining outputs' sensitivity to harvesting duration, see the Supporting information). Experiments were replicated 30 times at each harvest rate: a smaller sample of 10 and a larger sample size of 100 were also attempted for a selection of harvest rates (Supporting information); however, resulting dynamics did not differ significantly from a smaller sample of 30, and the time needed to run the simulations was substantially higher. Harvesting took place once a year in month 6: we simulated discrete harvesting (as opposed to continuous) to better approximate harvesting in the Beverton–Holt model.

In the Beverton–Holt model, simulations were run following methodology in Barychka et al. (2020) (Supporting information). We used discrete-time model formulation following the approach in Barnes (2002). Parameters $r_{\max}$ and K were derived from field observations and included uncertainty (Table 1).

Table 1. Summary of harvesting experiment in the Madingley and the Beverton–Holt models. In the Madingley, we reduced the size of the steps for harvest rates of 0.25–0.60 to examine the model's outputs and dynamics in more detail around the optimum harvest rates.

	Value	
Attribute	Madingley	Beverton–Holt
Target group	Duiker-like: 13–21 kg as adults and > 100 g as juveniles	Peters' duiker *Cephalophus callipygus* Bay duiker *Cephalophus dorsalis*
Traits	Endothermic herbivores	–
Harvest rate, φ	0.00–0.25 in steps of 0.05 0.25–0.60 in steps of 0.03 0.60–0.90 in steps of 0.10	0–0.90 in steps of 0.05
Example species	Peters' duiker *Cephalophus callipygus* Bay duiker *Cephalophus dorsalis*	–
Response metrics	Yields (animals km^{-2} year^{-1}) Survival probability (over 30 years) Change in ecosystem structure	Yields (animals km^{-2} year^{-1}) Survival probability (over 30 years)
Location(s)	1° × 1° geographic grid cell centred on 1°S, 15°E (Republic of Congo)	Studies from five main research areas: the Ituri Forest (Democratic Republic of Congo); Makokou (north-eastern Gabon); Bioko and Rio Muno (Cameroon); Dzanga-Sangha and Dzanga-Ndoki National Parks (Central African Republic), and Arabuko Sokoke (Kenya). Barychka et al. (2020) for more information.
Parameter values	–	Peters' duiker[1]: $\mu_{rmax} = 0.44$ $s_{rmax} = 0.14$ $\mu_K = 9.70$ $s_K = 3.62$ Bay duiker[1]: $\mu_{rmax} = 0.39$ $s_{rmax} = 0.14$ $\mu_K = 5.43$ $s_K = 2.55$

[1] Mean μ intrinsic rate of population increase, $r_{\max}$ and carrying capacity, K (animals km^{-2}), with 1 standard deviation (s) based on field data. N_0 represents starting population size and was set at $0.2K < N_0 < 0.8K$. Barychka et al. (2020) for more details about the Beverton–Holt model parameterisation.

We simulated proportional harvesting over 30 years with harvest rate φ ranging from 0 (no harvest) to 0.90 in discrete steps of 0.05, giving 19 different values of φ (Table 1). The share of the duiker-like animals actually harvested was equal to the number of animals in the group multiplied by the harvest rate φ, that is, 0–90% of the target group. For each combination of timescale and harvest rate, we carried out an ensemble of 1000 simulations. Harvesting was applied from year 1 onwards (no harvesting took place in year 0). The ensemble size was based on preliminary analysis involving comparing summary statistics and visualising results for smaller (100 simulations and 500 simulations) and larger (10 000 simulations) sample sizes. Based on model estimates, we assessed average yields, survival probability and the uncertainty in both yield and survival.

Output metrics

Yield

Using the Madingley model, total yields and target animal densities were recorded. The total yield in year t was $Y_{t,n} = \sum_1^c \sum_1^{n=30} y_{c,n}$, where $y_{c,n}$ was yield from harvesting cohort c in simulation n in month 6. The total density was

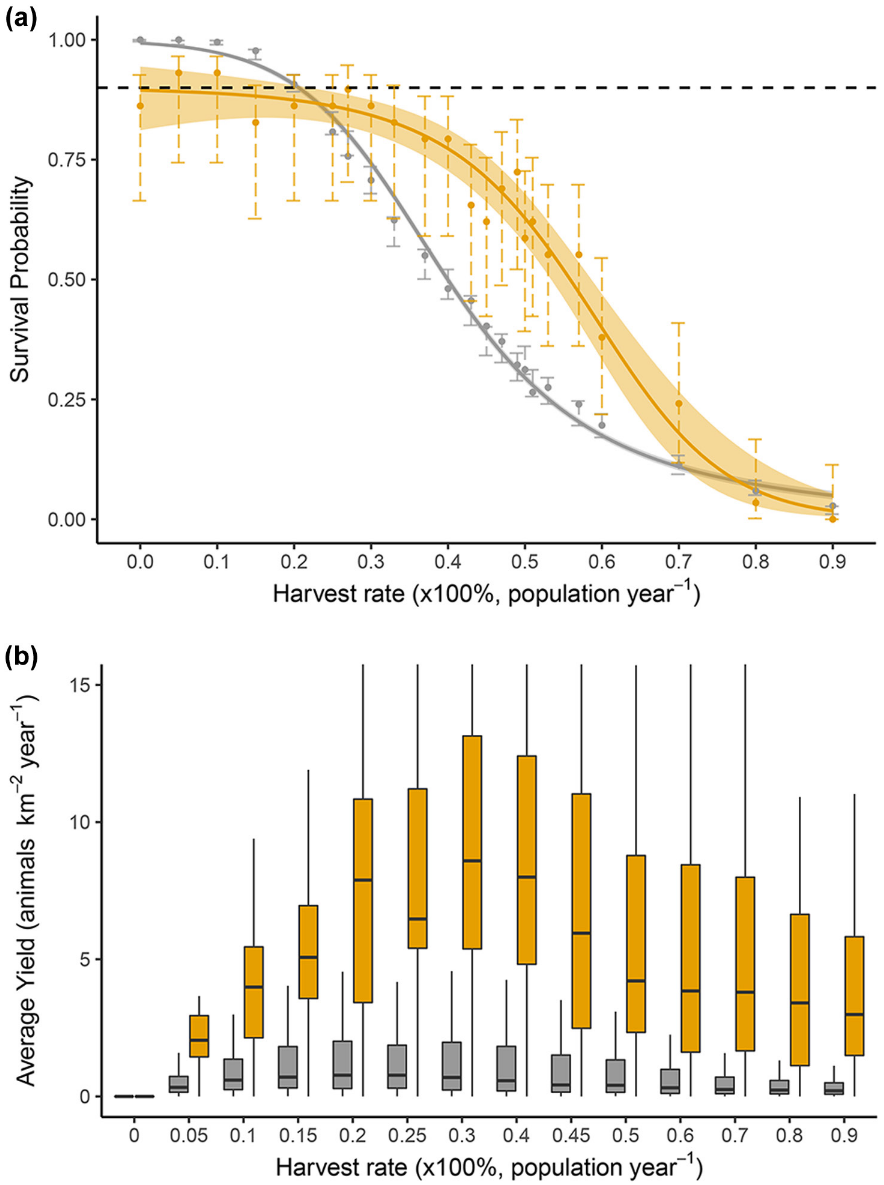

Figure 2. Survival probabilities (with 95% confidence intervals in grey/orange shading) in (a), and estimated yields in (b) from proportional harvesting of *C. callipygus* using the Beverton–Holt model (in grey), and of duiker-like herbivores (13–21 kg) using the Madingley general ecosystem model (in orange). The lines in (a) represent logistic regression model fitted to the data; points represent mean survival probabilities; vertical error bars show 2 standard errors from the mean. The horizontal dashed line indicates 90% survival target (i.e. extinction in less than 10% of the cases). Yields can be converted to biomass by multiplying by average body mass of 17 kg.

$D_{m,n} = \sum d_{m,c,n}$, where $d_{m,c,n}$ was density for target cohort c in simulation n in month m.

Using the Beverton–Holt model, yield at time $t(Y_t)$ was the difference between the number of animals at time t ($N_t^{\text{pre-harvest}}$ after reproduction at the end of year $t - 1$), and the higher of 0 and the number of surviving animals after target proportion φ of animals had been extracted at time t. I.e. $Y_t = N_t^{\text{pre-harvest}} - N_t^{\text{post-harvest}}$, where the number of animals that remain in the population after harvesting at time t, $N_t^{\text{post-harvest}} = \max(0, N_t^{\text{pre-harvest}} - \varphi \times N_t^{\text{pre-harvest}})$ (Barychka et al. 2020).

As a reminder, in the Madingley model, more than one species fell under our body-mass defined categorisation of duiker-like, and the model simulated an initial pristine ecosystem. Thus, a direct comparison between the Madingley and Beverton–Holt is not possible. For example, in addition to Peters' and bay duiker, water chevrotain *Hyemoschus aquaticus* with mean body mass of 15 kg, Ogilby's duiker *Cephalophus ogilbyi*, 19.5 kg, also fell into the duiker-like category. To at least help with the comparison, we added yields from harvesting bay duiker *C. dorsalis* to Peters' duiker yields from the Beverton–Holt models, providing a lower bound on the predicted yield from multi-species harvesting.

Extinction

The rate of extinction of duiker-like animals in the Madingley model was estimated at each time step. Extinction was defined when the total density ($D_{m,n}$) of animals that matched the definition of duiker-like fell below 0.1 animals km^{-2} during a simulation run. Duiker home range sizes are estimated at around 0.10 km^{-2} (Payne 1992). Therefore, this corresponds to approximately 99% reduction in density from average carrying capacity for Peters' and bay duiker (Feer 1988, Lahm 1993, van Vliet and Nasi 2008).

The same threshold (0.1 animals km^{-2}) was applied to estimate the two duiker species survival probability using the Beverton–Holt model. A response of 1 was assigned to a year where population size $N_t^{\text{post-harvest}}$ was equal to or above a threshold of 0.1 animals km^2; zero (0) was assigned to a year (and all subsequent years) when population size dipped below the viability threshold (we set $N_t^{\text{post-harvest}}$, i.e. quasi-extinction). Responses were then averaged to give an estimate of survival probability at each harvest rate with 95% confidence intervals over 30-year harvest. We used a minimum survival target of 90% of the population (Mace and Lande 1991) over the duration of harvesting as a benchmark. This level of extinction has been recommended as the highest acceptable level of risk if biological diversity is to be maintained at near-present levels for the foreseeable future (Mace and Lande 1991).

Ecosystem response

The ecosystem-level information was recorded in the Madingley at each time step, such as, for each functional group, adult body masses, animal biomasses and abundances.

Overall, the ecosystem-level response to harvesting was analysed as follows. First, each cohort's functional group (f) was identified as being a herbivore, omnivore or carnivore. Individuals were also allocated into a body mass bin (b) ranging from the smallest body mass (10^{-3} to 10^{-2} g; $b = -3$) to the largest bin (10^6–10^7 g; $b = 7$). Because some of the bins were deemed too wide to be able to capture changes in cohort abundances due to harvesting, bins were further sub-divided into smaller sub-bins, where adult body masses were incremented in steps of 0.5 for $2 \leq b \leq 6$. Total abundances were then calculated for each functional group in each body mass bin and logged (on $\log_{10}$ scale).

To account for temporal autocorrelation in animal abundances, changes in abundance due to harvesting were calculated as follows: change $\Delta_{m,n,f,b} = \text{Abundance}_{m,n,f,b}^{\text{Harvested}} - \text{Abundance}_{m,n,f,b}^{\text{Baseline}}$, where abundances are measured in month m, for functional group f (herbivore/omnivore/carnivore) in body mass bin b in simulation n. Here, we compared total animal abundances without harvesting ('baseline') to abundances where 20, 50, 70 and 90% ($\varphi = 0.2$, $\varphi = 0.5$, $\varphi = 0.7$ and $\varphi = 0.9$) of duiker-like population was targeted ('harvested'). In Fig. 3, we show the multiplicative difference between predictions of abundance change under the baseline and the harvesting regimes, e.g. 1 corresponds to no change in abundance, 2 corresponds to twice change in abundance (i.e. animal abundance where duiker-like are harvested are 2 times baseline abundance), 0.5 corresponds to 0.5 change in abundance (i.e. animal abundance where duiker-like are harvested are 0.5 of baseline abundance).

Results

Bushmeat yields and survival probability

The probability of extinction, and the optimal harvesting rates expected yields from harvesting duiker-like herbivores predicted by the Madingley model, were qualitatively (direction of changes, distinguishing attributes) and quantitatively (measured in terms of magnitude) similar to those predicted by the Beverton–Holt model, with a few notable differences.

Both models predicted a gradual decline in survival probability with increased harvesting (Fig. 2a). Extinctions were noticeably more common without harvesting and at very low harvesting pressure in the Madingley model than in the Beverton–Holt model (at $\varphi = 0$ survival probability of 0.86 ± 0.13 and 0.99 ± 0.001; 95% CI, respectively). In the Beverton–Holt model extinction rate increased more strongly at $\varphi \geq 0.15$. The opposite was true at intermediate and high levels of harvesting, where survival rates were significantly higher in the Madingley than in the Beverton–Holt model. Both models estimated the annual harvesting rate of $\varphi > 0.2$ ($\varphi = 0.2$ and $\varphi = 0.2$–0.25 in the Madingley and the Beverton–Holt model, respectively) could result in a high risk of extinction.

In both models, expected yield had a single peak at intermediate extraction rates (Fig. 2b, Supporting information). Yields were maximised at an annual harvest rate of

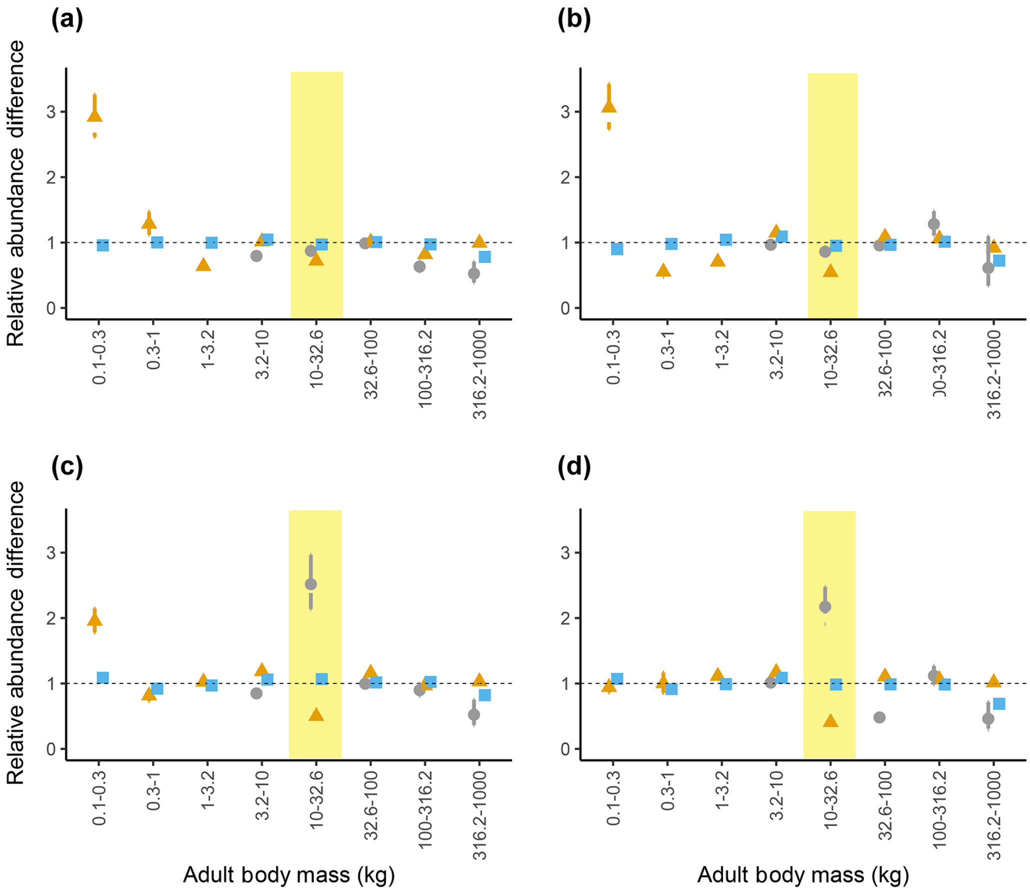

Figure 3. Relative change in abundance (with 95% confidence intervals) of endothermic heterotrophs: herbivores (orange triangles), omnivores (blue squares) and carnivores (grey circles), as a result of harvesting duiker-like herbivores (10–32.6 kg group highlighted in yellow) at the rate of (a) 20%, (b) 50%, (c) 70% and (d) 90% of population year^{-1}, by adult body mass. The horizontal dashed line indicates no significant impact of harvesting on abundances.

$\varphi = 0.25$–0.3 ($\varphi = 0.25$ and $\varphi = 0.3$ in the Beverton–Holt and the Madingley, respectively). The interquartile ranges for yields did not overlap: the Madingley's median yields were on average 11.67 ± 1.49 (95% CI, n = 30) times higher than the Beverton–Holt's, and 4.64 ± 0.44 (95% CI, n = 30) times higher if mean yields were compared (Beverton–Holt's yields were strongly right-skewed). In relative terms, the Madingley average yields were less variable than the Beverton–Holt's; for example, at $\varphi = 0.3$ the interquartile range was 2.3 times the median value (IQR = 1.8, median = 0.78) for the Beverton–Holt model and 0.9 times the median value (IQR = 7.8, median = 8.59) for the Madingley model.

When we added yields from harvesting bay duiker *C. dorsalis* to Peters' duiker from the Beverton–Holt models, the difference between the two models fell by half: to 5.35 ± 0.66 times for the median yields, and to 2.71 ± 0.35 times for the mean yields. Given that the two modelling approaches are so very different (Supporting information), we considered a match to within a factor of 5 to be sufficient to motivate further examination of the Madingley model predictions.

Ecosystem impacts of harvesting duiker-like animals

At four levels of harvesting intensity ($\varphi = 0.2$, $\varphi = 0.5$, $\varphi = 0.7$ and $\varphi = 0.9$) of the duiker-like herbivores, there were a few general patterns in ecosystem responses to harvesting compared to the baseline (Fig. 3). Harvesting at $\varphi > 0.2$ (i.e. above 20% of duiker-like population) resulted in significant declines in duiker-like abundances (highlighted in yellow in Fig. 3): on average, a relative abundance difference of 0.72 in duiker-like abundances was expected at $\varphi = 0.2$, and a relative abundance difference of 0.41 in duiker-like abundances at $\varphi = 0.9$.

Harvesting duiker-like animals resulted in a number of changes in ecosystem structure. In particular, the model predicted increases in relative abundance of up to 3.1 in small-bodied (0.1–0.3 kg) herbivores at low and medium-high levels of duiker-like harvesting ($\varphi \leq 0.7$; Fig. 3a–c). The relative abundance of small-bodied herbivores remained unchanged at very high harvest rates ($\varphi = 0.9$; Fig. 3d). The relative abundance of medium-sized (10–32.6 kg) carnivores increased at high harvest rates ($\varphi \geq 0.7$; Fig. 3c–d). While large-bodied carnivores and omnivores (316–1000 kg) were negatively affected by duiker-like harvesting, with a relative abundance difference of 0.53–0.75 on average.

Discussion

Summary

Our results illustrate how the Madingley model might potentially be used to inform bushmeat harvesting. A major advantage of the Madingley model in this regard is that it can make predictions for poorly-studied species, that is those with no available field data or parameter estimates. However, in this research, we chose to make predictions for a relatively well-studied species, in order to facilitate a model–model comparison of the Madingley model predictions, with those of a single-species model, based on field data, for this same species. This model–model comparison can inform our understanding of the strengths, weaknesses and uncertainties of the Madingley model when used for this purpose.

We found both models estimated the optimal harvest rate at 20–25% ($\varphi = 0.2$–0.25) of the duiker population per year; and predicted qualitatively similar curves relating extinction to harvest rate. The predictions for sustainable yield were within a factor of 5. We therefore consider that overall the degree of match in the predictions illustrates that general ecosystem models, such as the Madingley model, have now developed to the point where they are potentially useful in informing bushmeat policy.

Model–model comparison

The Madingley model yields were around five times greater than the yield predicted by summing the Beverton–Holt models for the two duiker species. Although significant, we nonetheless consider this result to be encouraging for several reasons. First, the sum over the Beverton–Holt models represents a lower bound on the predicted yields from single-species models, because it does not include other species that would fall into the same functional group and size range in reality, and in the Madingley model. Second, the Madingley simulations being with a truly pristine ecosystem, whereas the Beverton–Holt parameters are estimated from locations where humans have significantly impacted the ecosystems for thousands of years. Third, the Beverton–Holt predictions are themselves highly uncertain, reflecting parameter uncertainty (Barychka et al. 2020). Fourth, the Beverton–Holt predictions, and the Madingley model predictions, were generated from methodologies that are very different, with the former employing a very simple model with species-specific parameters, and the latter employing a complex simulation model with climate as the only input (Supporting information).

On the other hand, a factor of 5 mismatch is obviously substantial in terms of the implied economic and nutrition value of bushmeat harvesting on the ground. This degree of mismatch highlights the importance of exploring the use of multiple models and approaches to inform bushmeat policy, as part of a wider process, whereby stakeholders actively discuss, challenge and weigh up different sources of guidance and evidence (Milner-Gulland and Bennett 2003, Bennett et al. 2007, Hurst 2007). Some might consider that the factor of 5 mismatch in predicted yield is large enough to discount the Madingley model predictions entirely. Others might conclude that the predicted yields should be discounted but take note of the predicted extinction probability and/or wider ecosystem impacts. Either way, model–model comparisons, such as presented here, help to allow stakeholders to make a more informed choice of which sources of evidence to consider.

Local extinction

The 10% extinction rate without harvesting in the Madingley (Fig. 2a), which was not represented in the Beverton–Holt model, is arguably more realistic in reflecting the effects of environmental and demographic stochasticity that are absent in the Beverton–Holt (Lande et al. 1995, 1997, Bousquet et al. 2008). Although stochasticity could be easily added to a single-species model (Jonzén et al. 2002, Lande 1998), as we have done here with low-level environmental stochasticity, it emerges more realistically in the Madingley model as a result of interactions between and within trophic groups, and with their environment (Supporting information). Similarly, higher population persistence rates in the Madingley model than in the Beverton–Holt at moderate and high rates of harvesting were arguably more representative of real-life ecosystems, as: a) smaller animals would be more likely to avoid capture and reproduce (Wilkie and Finn 1990), and b) predators would switch between similar-sized prey species as they became more rare (Allen 1988). In addition, as more desirable prey species become rare, hunters may switch to less desirable species (Wright et al. 2000) – although this behaviour was not modelled here, it could affect species persistence in real-life ecosystems. The population persistence dynamics revealed that keeping the risk of extinction below a maximum acceptable level of 10% on average (Mace and Lande 1991) implied harvesting not more than 20% of duiker-like population year^{-1} – a rather low harvest rate, implying a trade-off that decision-makers may need to consider. Adopting higher risk levels, for example, 20% probability of extinction (or 50%) over the harvesting period (Mace and Lande 1991), would result in an optimal harvest rate of 0.3–0.4 (or 0.5) for the Madingley model and of 0.25–0.27 (or 0.4) for the Beverton–Holt model. The risk threshold could depend on stakeholders degree of risk aversion, harvested species or duration of harvesting horizon (Mace and Lande 1991, Barychka et al. 2020). Importantly, the management strategy applied to all animals within the duiker-like target group which was made of an assortment of species some of which could be more or less robust to the simulated harvest regime. The Madingley's 10% extinction rate representing background extinctions absent in a single-species model should be taken into consideration by policy-makers who may need to adopt relative rather than absolute extinction thresholds.

Wider ecosystem impacts

Here, the Madingley model was used to predict the effect of harvesting on ecosystem structure. Removing duiker-like herbivores had relatively low impacts on other functional groups, with the exception of small-bodied herbivores (which would likely compete with duikers for resources) and large-bodied predators. However, duiker-like herbivores contributed only between 2% and 4% of total abundance of similar-sized animals in the Madingley model, which could also explain this relatively low impact.

Studies of biological consequences of over-hunting on species in African tropical forest ecosystems generally focus only on the target species; declines in density were recorded in duikers and other mammals (Fitzgibbon et al. 1995, Gates 1996, Noss 1998b). In terms of effects of removal of target species on non-target animal groups; very high abundances of common opossums *Didelphis marsupialis* and spiny rats *Proechimys* spp. were reported in heavily fragmented forests of Brazil and central Panama, explained by the absence of their predators and/or competitors (da Fonseca and Robinson 1990, Adler 1996). Fa and Brown (2009) predicted that the abundance of non-target small and medium-sized species could remain unchanged or even increase depending on the availability of their prey and removal of competitors and other predators. According to (Wright et al. 2000), large-bodied species preferred by hunters would decline with harvesting pressure; the less desirable species would first increase due to lower competition for resources, and then decline; and small untargeted species would increase steadily. The trophic cascades theory predicts that higher abundances of mid-level consumers should result in lower abundance of basal producers (assuming 'top–down' control) (Pace et al. 1999, Kennedy 2012, Palmer et al. 2015). However, changes in higher trophic levels do not always propagate to lower levels or have significant ecosystem impacts; higher resilience to perturbations is possible in systems with high trophic diversity and complex food webs (Pace et al. 1999, Wright 2003).

From the point of view of a bushmeat manager considering the wider ecosystem impacts of harvesting, the system, as indicated by the Madingley model, was relatively robust to intensive harvesting. Many animals were heavily depleted but did not become extinct, smaller-bodied animals increased in abundance, and vacant ecological niches were being quickly filled-in by, presumably, more resilient faster-reproducing animals (da Fonseca and Robinson 1990, Adler 1996). However, harvesting intensively also resulted in a very different ecosystem structure (Scheffer et al. 2001), dominated by small-bodied short-lived animals. Considering the tradeoff between high yields now, and lower yields, lower species diversity, and a different ecosystem structure and functioning later, should be a part of decision-making process in bushmeat management.

Limitations

There were several key limitations of our modelling approach. Our harvesting protocol was relatively simple. Our methodology guaranteed that the assigned proportion (varied from 0 to 90%) of the duiker-like target group were harvested each harvesting round. Harvesting was applied to a single location approximately 100 × 100 km; no inter-cell migration was allowed. Although duiker home ranges are relatively small, around 0.10 km^{-2} (Payne 1992), in reality, local duiker populations would likely disperse (depending on strength of pressure on neighbouring ecosystems) and therefore replenish nearby areas, most likely then increasing species overall tolerance to pressure (Fa and Brown 2009). Although we used carrying capacities from unhunted sites, these were likely to be below truly pristine ecosystems levels. Using the Madingley-derived functional-group-wide densities could help address the multi-species context and human-induced reductions in animal densities, and therefore might allow better reconciliation of the models. This could also be a useful additional step for investigating the causes of differences between the models. We assumed constant non-adaptive harvesting which was not affected by the return per unit effort, the selectivity of hunters (Wright 2003), or any other socioeconomic factors such as proximity to roads or access to salaried employment (Nielsen 2006, Nielsen et al. 2014). No provision was made in the model for the potential wastage due to animals captured and discarded as unsuitable for sale or consumption, or animals escaping after being injured (and likely dying later on), though it could add a quarter to recorded harvesting mortality (Noss 1998b).

Future directions

The Madingley model's main strengths are its generality and ability to look at any functional species group and location, including ones that have not yet been studied in any detail and thus are lacking in data (Purves et al. 2013, Bartlett et al. 2016). Here, we used the model on one of the most common and best-studied bushmeat species, so that we could compare the Madingley model results to those from traditional methods. The Madingley model was able to produce reasonable estimates for duiker-like harvesting dynamics based solely on climate data and given ecological processes. The discrepancies between the models may be reduced further by adjusting parameters of the Beverton–Holt model, in particular, its starting population densities. Successful tests would be a useful additional step for investigating the causes of differences between the models and could provide a further compelling argument for ecosystem-based models.

The Madingley model can be used in locations and for species with no available empirical data; however, in many cases some data and/or other models are available. This raises the possibility of combining the Madingley model and these other sources of information into hybrid approaches. This could be done informally, as part of weighing up sources of information during stakeholder process, or formally, by plugging any available data (for example, density estimates) into the Madingley model, or using the Madingley to provide parameters for simpler models. Investigating harvesting outcomes for multiple species and locations could provide further information about the model's potential as a predictive tool for harvest management.

The aim was to test an ecosystem-based model against a simple single-species model parameterised with empirical data. While the Beverton–Holt model was able to capture the salient features of single-species harvesting (Fryxell et al. 2010), in the absence of population parameter estimates the Madingley model could be used to offer adequate indication of harvesting outcomes. Therefore, the main value may come from using the Madingley model (or models like it) for location and species that have been barely studied at all.

Moreover, there is a lack of understanding of synergies and interactions within ecosystems (da Fonseca and Robinson 1990, Wright 2003) which we may not be able to address using traditional modelling for some time. Predicting dynamics and potential impacts of multi-species harvesting has not been considered feasible for many real-life populations (Hooper et al. 2005). These results suggest that in the absence of well-informed empirical models mechanistic models such as the Madingley general ecosystem model could provide helpful approximations of such dynamics.

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Statement of authorship – TB performed the modelling work, analysed the output data and led the writing of the manuscript. The concept and design of experiment was revised by all authors. All authors contributed substantially to revisions.

Author contributions

Georgina M. Mace sadly died 19 September 2020. **Tatsiana Barychka**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Georgina M. Mace**: Conceptualization (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Drew W. Purves**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

The Madingley model is publicly available on <https://madingley.github.io/>. The simulation outputs will be deposited in DataDryad: <http://dx.doi.org/10.5061/dryad.1g1jwstxh> (Barychka et al. 2021).

References

Abernethy, K. A. et al. 2013. Extent and ecological consequences of hunting in Central African rainforests in the twenty-first century. – Phil. Trans. R. Soc. B 368: 20120303.

Adler, G. 1996. The island syndrome in isolated populations of a tropical forest rodent. – Oecologia 108: 694–700.

Albrechtsen, L. et al. 2007. Faunal loss from bushmeat hunting: empirical evidence and policy implications in Bioko Island. – Environ. Sci. Policy 10: 654–667.

Alkemade, R. et al. 2009. GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. – Ecosystems 12: 374–390.

Allen, J. A. 1988. Frequency-dependent selection by predators. – Phil. Trans. R. Soc. B 319: 485–503.

Barnes, R. F. W. 2002. The bushmeat boom and bust in West and Central Africa. – Oryx 36: 236–242.

Barnes, R. F. W. and Lahm, S. A. 1997. An ecological perspective on human densities in the Central African Forest. – J. Appl. Ecol. 34: 245–260.

Bartlett, L. J. et al. 2016. Synergistic impacts of habitat loss and fragmentation on model ecosystems. – Proc. R. Soc. B 283: 20161027.

Barychka, T. et al. 2020. Modelling parameter uncertainty reveals bushmeat yields versus survival trade-offs in heavily-hunted duiker *Cephalophus* spp. – PLoS One 15: e0234595.

Barychka, T. et al. 2021. Data from: The Madingley general ecosystem model predicts bushmeat yields, species extinction rates and ecosystem-level impacts of bushmeat harvesting. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.1g1jwstxh>.

Bennett, E. L. et al. 2007. Hunting for consensus: reconciling bushmeat harvest, conservation and development policy in West and Central Africa. – Conserv. Biol. 21: 884–887.

Beverton, R. J. H. and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fisheries investigation series 2, volume 19, UK Ministry of Agriculture. – Fisheries and Food, London, UK.

Bhattacharya, D. K. and Begum, S. 1996. Bionomic equilibrium of two-species system. I. – Math. Biosci. 135: 111–127.

Bodmer, R. E. et al. 1997. Linking conservation and local people through sustainable use of natural resources: community-based management in the Peruvian Amazon. – In: Freese, C. H. (ed.), Harvesting wild species: implications for biodiversity conservation. Johns Hopkins University Press, pp. 315–358.

Bousquet, N. et al. 2008. Redefining the maximum sustainable yield for the Schaefer population model including multiplicative environmental noise. – J. Theor. Biol. 254: 65–75.

Brodie, J. F. 2016. How monkeys sequester carbon. – Trends Ecol. Evol. 31: 414–416.

Case, T. J. 2000. An illustrated guide to theoretical ecology. – Oxford Univ. Press.

Christensen, V. and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. – Ecol. Model. 172: 109–139.

Coad, L. et al. 2019. Towards a sustainable, participatory and inclusive wild meat sector. – CIFOR.

da Fonseca, G. A. B. and Robinson, J. G. 1990. Forest size and structure: competitive and predatory effects on small mammal communities. – Biol. Conserv. 53: 265–294.

Davies, G. and Brown, D. 2008. Bushmeat and livelihoods: wildlife management and poverty reduction. – Wiley.

Effiom, E. O. et al. 2013. Bushmeat hunting changes regeneration of African rainforests. – Proc. R. Soc. B 280: 20130246.

Fa, J. E. and Brown, D. 2009. Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. – Mammal Rev. 39: 231–264.

Fa, J. E. and Peres, C. A. 2001. Game vertebrate extraction in African and Neotropical forests: an intercontinental comparison. – In: Conservation biology series. Cambridge Univ. Press, pp. 203–241.

Fa, J. E. et al. 1995. Impact of market hunting on mammal species in Equatorial Guinea. – Conserv. Biol. 9: 1107–1115.

Fa, J. E. et al. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. – Biol. Conserv. 121: 167–176.

Fa, J. E. et al. 2014. Integrating sustainable hunting in biodiversity protection in Central Africa: hot spots, weak spots and strong spots. – PLoS One 9: e112367.

Fa, J. E. et al. 2016. Differences between pygmy and non-pygmy hunting in Congo Basin forests. – PLoS One 11: e0161703.

Feer, F. 1988. Stratégies écologiques de deux espèces de Bovidés sympatriques de la forêt sempervirente africaine (*Cephalophus callipygus* et *C. dorsalis*): influence du rythme d'activité. – PhD thesis, Univ. Pierre et Marie Curie, Paris, France.

Fitzgibbon, C. D. et al. 1995. Subsistence hunting in Arabuko-Sokoke Forest, Kenya and its effects on mammal populations. – Conserv. Biol. 9: 1116–1126.

Flores, C. et al. 2019. Food webs: insights from a general ecosystem model. – BioRxiv: 588665. <http://biorxiv.org/content/early/2019/03/26/588665>.

Foerster, S. et al. 2011. Correlates of bushmeat hunting among remote rural households in Gabon, Central Africa. – Conserv. Biol. 26: 335–344.

Fryxell, J. M. et al. 2010. Resource management cycles and the sustainability of harvested wildlife populations. – Science 328: 903–906.

Fulton, E. A. et al. 2004. Ecological indicators of the ecosystem effects of fishing. – Final Report. Report No. R99/1546, Australian Fisheries Management Authority, Canberra.

Fulton, E. A. et al. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. – Fish Fish. 12: 171–188.

Gates, J. F. 1996. Habitat alteration, hunting and the conservation of folivorous primates in African forests. – Aust. J. Ecol. 21: 1–9.

Golden, C. D. et al. 2011. Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. – Proc. Natl Acad. Sci. USA 108: 19653–19656.

Goodall, D. W. 1975. Ecosystem modeling in the desert biome. – Syst. Anal. Simul. Ecol. 3: 73–94.

Harfoot, M. B. J. et al. 2014. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. – PLoS Biol. 12: e1001841.

Hart, J. A. 2000. Impact and sustainability of indigenous hunting in the Ituri Forest, Congo-Zaire: a comparison of unhunted and hunted duiker populations. – In: Robinson, J. G. and Bennet, E. (eds), Hunting for sustainability in tropical forests. Columbia Univ. Press, pp. 106–153.

Holden, M. H. and Conrad, J. M. 2015. Optimal escapement in stage-structured fisheries with environmental stochasticity. – Math. Biosci. 269: 76–85.

Hooper, D. U. et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecol. Monogr. 75: 3–35.

Hurst, A. 2007. Institutional challenges to sustainable Bushmeat management in Central Africa. – In: Davies, G. and Brown, D. (eds), Bushmeat and livelihoods: wildlife management and poverty reduction. Wiley, pp. 158–171.

Hutniczak, B. 2015. Modeling heterogeneous fleet in an ecosystem based management context. – Ecol. Econ. 120: 203–214.

Ingram, D. J. 2018. Quantifying the exploitation of terrestrial wildlife in Africa. – PhD thesis, Univ. of Sussex, UK.

Jonzén, N. et al. 2002. A theory of stochastic harvesting in stochastic environments. – Am. Nat. 159: 427–437.

Kennedy, M. S. 2012. Trophic cascades: predators, prey and the changing dynamics of nature. – Austral Ecol. 37: e9–e10.

Lahm, S. A. 1993. Ecology and economics of human/wildlife interaction in northeastern Gabon. – PhD thesis, New York Univ.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. – Resear. Popul. Ecol. 40: 259–269.

Lande, R. et al. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. – Am. Nat. 145: 728–745.

Lande, R. et al. 1997. Threshold harvesting for sustainability of fluctuating resources. – Ecology 78: 1341–1350.

Leclère, D. et al. 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. – Nature 585: 551–556.

Linder, J. 2008. Differential vulnerability of primates to hunting in Korup National Park, Cameroon: implications for primate conservation. – City Univ. of New York.

Link, J. S. et al. 2010. The northeast US application of ATLANTIS: a full system model exploring marine ecosystem dynamics in a living marine resource management context. – Prog. Oceanogr. 87: 214–234.

Mace, G. M. and Lande, R. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. – Conserv. Biol. 5: 148–157.

Metzgar, L. et al. 2013. Total ecosystem model for a cove in Lake Texoma. – Syst. Anal. Simul. Ecol. 3: 205–205.

Milner-Gulland, E. J. and Akçakaya, H. R. 2001. Sustainability indices for exploited populations. – Trends Ecol. Evol. 16: 686–692.

Milner-Gulland, E. J. and Bennett, E. L. 2003. Wild meat: the bigger picture. – Trends Ecol. Evol. 18: 351–357.

Nasi, R. et al. 2011. Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. – Int. For. Rev. 13: 355–368.

Newbold, T. et al. 2020. Non-linear changes in modelled terrestrial ecosystems subjected to perturbations. – Sci. Rep. 10: 1–10.

Nielsen, M. R. 2006. Importance, cause and effect of bushmeat hunting in the Udzungwa Mountains, Tanzania: implications for community based wildlife management. – Biol. Conserv. 128: 509–516.

Nielsen, M. R. et al. 2014. Factors determining the choice of hunting and trading bushmeat in the Kilombero Valley, Tanzania. – Conserv. Biol. 28: 382–391.

Njiforti, H. L. 1996. Preferences and present demand for bushmeat in north Cameroon: some implications for wildlife conservation. – Environ. Conserv. 23: 149–155.

Noss, A. J. 1998a. The impacts of BaAka net hunting on rainforest wildlife. – Biol. Conserv. 86: 161–167.

Noss, A. J. 1998b. The impacts of cable snare hunting on wildlife populations in the forests of the Central African Republic. – Conserv. Biol. 12: 390–398.

Noss, A. J. 2000. Cable snares and nets in the Central African Republic. – In: Robinson, J. G. and Bennet, E. (eds), Hunting for sustainability in tropical forests. Columbia Univ. Press, pp. 282–304.

Pace, M. L. et al. 1999. Trophic cascades revealed in diverse ecosystems. – Trends Ecol. Evol. 14: 483–488.

Palmer, G. et al. 2015. Nationwide trophic cascades: changes in avian community structure driven by ungulates. – Sci. Rep. 5: 15601–15601.

Payne, J. C. 1992. Field study of techniques for estimating densities of duikers in Korup National Park, Cameroon.

Peres, C. A. 2000. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian forest sites. – In: Robinson, J. G. and Bennet, E. (eds), Hunting for sustainability in tropical forests. Columbia Univ. Press, pp. 31–56.

Peres, C. A. and Dolman, P. M. 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. – Oecologia 122: 175–189.

Purves, D. et al. 2013. Time to model all life on Earth. – Nature 493: 295–295.

Robinson, J. G. and Redford, K. H. 1991. Sustainable harvest of neotropical forest mammals. – In: Robinson, J. and Redford, K. H. (eds), Neotropical wildlife use and conservation, Univ. of Chicago Press, pp. 415–429.

Rodríguez, J. P. et al. 2007. The application of predictive modelling of species distribution to biodiversity conservation. – Divers. Distrib. 13: 243–251.

Scheffer, M. et al. 2001. Catastrophic shifts in ecosystems. – Nature 413: 591–596.

Schipper, A. M. et al. 2020. Projecting terrestrial biodiversity intactness with GLOBIO 4. – Global Change Biol. 26: 760–771.

Song, X. and Chen, L. 2001. Optimal harvesting and stability for a two-species competitive system with stage structure. – Math. Biosci. 170: 173–186.

Taylor, G. et al. 2015. Synthesising bushmeat research effort in West and Central Africa: a new regional database. – Biol. Conserv. 181: 199–205.

Travers, M. et al. 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. – Prog. Oceanogr. 75: 751–770.

van Vliet, N. and Nasi, R. 2008. Why do models fail to assess properly the sustainability of duiker (*Cephalophus* spp.) hunting in Central Africa? – Oryx 42: 392–399.

Van Vliet, N. et al. 2007. Evidence for the local depletion of bay duiker *Cephalophus dorsalis*, within the Ipassa Man and Biosphere Reserve, north-east Gabon. – Afric. J. Ecol. 45: 440–443.

van Vliet, N. et al. 2015. Bushmeat consumption among rural and urban children from Province Orientale, Democratic Republic of Congo. – Oryx 49: 165–174.

Van Vliet, N. et al. 2017. Bushmeat and human health: assessing the evidence in tropical and sub-tropical forests. – Ethnobiol. Conserv. 6: 1–45.

Weinbaum, K. Z. et al. 2013. Searching for sustainability: are assessments of wildlife harvests behind the times? – Ecol. Lett. 16: 99–111.

Wilkie, D. S. and Carpenter, J. F. 1999. Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. – Biodivers. Conserv. 8: 927–955.

Wilkie, D. S. and Finn, J. T. 1990. Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaire. – Biotropica 22: 90–99.

Wilkie, D. S. et al. 2001. Defaunation, not deforestation: commercial logging and market hunting in northern Congo. – Columbia Univ. Press, pp. 375–400.

Wright, S. J. 2003. The myriad consequences of hunting for vertebrates and plants in tropical forests. – Perspect. Plant Ecol. Evol. Syst. 6: 73–86.

Wright, S. J. et al. 2000. Poachers alter mammal abundance, seed dispersal and seed predation in a Neotropical forest. – Conserv. Biol. 14: 227–239.

Yodzis, P. 1994. Predator–prey theory and management of multispecies fisheries. – Ecol. Appl. 4: 51–58.