

# A bioeconomic analysis of bushmeat hunting

R. Damania<sup>1\*</sup>, E. J. Milner-Gulland<sup>2</sup> and D. J. Crookes<sup>2</sup>

<sup>1</sup>*School of Economics, University of Adelaide, Adelaide 5001, Australia*

<sup>2</sup>*Department of Environmental Science and Technology, Imperial College London, Exhibition Road, London SW7 2AZ, UK*

Unsustainable bushmeat hunting is a major threat to mammal species, particularly in West/Central Africa. We developed a multispecies dynamic simulation model of hunter behaviour, parameterized using data from the Ashanti region, Ghana. The model distinguishes between two hunting techniques, snaring and gun hunting. We analyse the impact of key economic parameters on off-takes. Economic incentives determine the effort devoted to hunting, the choice of hunting technique, and the species that are consumed domestically or traded in markets. These factors, together with the growth rates and catchabilities of hunted species, determine the ecological impact of hunting. The results suggest that increased bushmeat prices are likely to lead to a switch from snaring, which is cheaper but less efficient, to gun hunting, with a consequent impact on vulnerable species. Increases in agricultural prices have an ambiguous effect on hunter behaviour, depending on the balance between incentives to invest in agriculture and increased consumption as incomes improve. Penalties are more effective if they target bushmeat sales, rather than the act of hunting. This model represents a step forward because it explicitly considers bushmeat as a component of the household economy. This has important implications as regards the development of policies to conserve species hunted for bushmeat.

**Keywords:** Ashanti; Ghana; snaring; gun hunting; agriculture; household economy

## 1. INTRODUCTION

Bushmeat hunting threatens the survival of many forest mammal species, particularly in West/Central Africa (Robinson & Bennett 2000; Bakarr *et al.* 2001). It is of current concern for a range of reasons including rising demand from an urbanizing population as incomes improve, human population growth and expansion into previously remote forest areas, the spread of more efficient technologies such as guns, and populations of particular species reaching critically low levels (Milner-Gulland *et al.* 2003). However, hunting is apparently sustainable in some areas, either because vulnerable species have already been extirpated (Cowlshaw *et al.* 2005) or because hunting pressure remains low (Hill & Padwe 2000). Bushmeat hunting is not only important in a conservation context, but is also a major component of people's livelihoods (de Merode *et al.* 2004). It is argued both that this is of concern, given that livelihoods are tied to a rapidly depleting resource (Bennett 2002; Fa *et al.* 2003), and that bushmeat hunting could contribute to development if managed for sustainability and transparently integrated into the general economy (Brown 2003).

Many bushmeat hunters also farm (Ntiemoa-Baidu 1998; Mendelson *et al.* 2003). Farmers may trap bushmeat around their fields for both home consumption and local sale. Others hunt commercially with guns and sell the majority of their produce in urban markets (Ntiemoa-Baidu 1998). Hence the amount of time devoted to hunting and the equipment used is a decision taken in the context of the household's other income-generating activities. The role of bushmeat hunting within the household economy is a crucial issue that has received little quantitative attention beyond a few empirical studies (e.g. de Merode

*et al.* 2004). However, the success of policy recommendations for the management of bushmeat hunting is dependent on the effects that control measures have on the hunting–farming decision. These measures may include altering bushmeat prices, penalties for hunting protected species, or raising agricultural prices.

Here, we examine the role of bushmeat hunting within the household economy, when households can invest their limited productive time in hunting or agriculture and when hunting involves two technologies; snares or guns. We follow the conceptual framework outlined by Damania *et al.* (2003). First, we develop a simple model of household behaviour, and then parameterize the model using data from the Ashanti region, Ghana.

## 2. THE MODEL

We focus on farm households engaging in production and consumption. There are two production activities: farming and bushmeat hunting. We assume that all agricultural output and a fraction of the bushmeat is sold in markets at given prices. The remainder of the bushmeat is consumed at home. Although we assume no home consumption of agricultural produce, the results generalize to the case in which a proportion of this produce is consumed at home. Income from bushmeat and crop sales is used to purchase food and other commodities. We distinguish between two widely used hunting techniques—hunting with snares and guns. The simulations suggest that this distinction is of both biological importance and economic significance (see also Rowcliffe *et al.* 2003).

There are  $i = 1, 2, \dots, I$  potentially hunted species, which may be captured by means of snares or guns. The total number of individuals of these species caught in snares is  $H_i^S$ , and  $H_i^G$  is the total number of individuals of these species killed with guns. A fraction  $\gamma_i \in [0, 1]$  of the off-take

\* Author for correspondence (richard.damania@adelaide.edu.au).

is consumed by the household and the remainder  $(1 - \gamma_i)$  is sold. Household utility is represented by a Cobb–Douglas function:

$$U = \alpha_F \ln(F) + \alpha_h \ln \sum_{i=1}^I \gamma_i (H_i^G + H_i^S), \quad (2.1)$$

where  $\alpha_F + \alpha_h = 1$ ;  $F$  is a composite consumption commodity. By equation (2.1) household utility depends on consumption of the composite good and bushmeat. Other more complex and realistic specifications of the utility function that incorporate income smoothing, seasonality or subsistence needs can be adopted. However, for simplicity we use the common Cobb–Douglas specification, leaving these complications for future research. Utility is maximized subject to the budget constraint:

$$\begin{aligned} p_q Q + \sum_{i \in H} (1 - \gamma_i) (p_i H_i^G - \delta_i t_i^G) + \sum_{i \in S} (1 - \gamma_i) (p_i H_i^S - \delta_i t_i^S) \\ = p_f F + \sum_{i \in I} \gamma_i \delta_i \theta (H_i^G + H_i^S + K) + C_G \sum_{i \in I} H_i^G + C_S \sum_{i \in I} H_i^S, \end{aligned} \quad (2.2a)$$

where superscript  $S$  denotes species hunted with snares and superscript  $G$  denotes species hunted with guns. The agricultural output is  $Q$ ,  $p_r$  ( $r = q, f, v$ ) is the price of good  $r$ , net of transport costs, and  $\delta_i$  is an indicator variable taking the value 1 if the species is protected and there is a penalty for hunting, and zero otherwise. We allow for the possibility that the expected penalty on sold bushmeat may differ from that on domestically consumed bushmeat, because bushmeat sold on open markets is more likely to be detected than that consumed at home. The probability of detecting a protected species at the hunting stage is  $\theta$ , and  $\rho$  is the probability of detection during sale. Hence  $\mu = \rho(1 - \theta)$  is the probability of detecting the protected species when it is sold, given that the hunter has not been detected while hunting. The fine is  $K$ . The expected penalty when protected species are sold is  $t_i^j = (\theta + \mu)(H_i^j + K)$ . The hunting cost parameter is  $C_j$  ( $j = S, G$ ), assumed to be linear on the basis of the survey data used in the simulations. We assume that bushmeat is a normal commodity. Little research has been carried out on elasticities of demand for bushmeat in Africa, and the evidence that exists is ambiguous.

Following Barrett & Arcese (1998), agricultural output depends on labour inputs with elasticity  $\beta$ .

$$Q = L_q^\beta, \quad (2.2b)$$

where  $L_q$  is labour time devoted to agriculture.

The gun hunting production function is defined by:

$$H_i^G \equiv \frac{N_i}{A} g_i^\rho L_G^{b_i}, \quad (2.2c)$$

where  $N_i$  is the biomass of species  $i$ ,  $A$  is the hunting area,  $g_i$  is group size of species  $i$ ,  $L_G$  is labour time devoted to gun hunting, and  $\rho$  and  $b_i$  are parameters. Equation (2.2c) is taken from Rowcliffe *et al.* (2003), and implies that the probability of an encounter with a species depends upon the density of the species  $N_i/A$ , the group or herd size ( $g_i$ ) and labour inputs ( $L_G$ ).

Snares captures are defined by:

$$H_i^S = (1 - e^{-2Dv_i N_i}) L_S, \quad (2.2d)$$

Equation (2.2d) is also taken from Rowcliffe *et al.* (2003), and it implies that the probability of capturing an animal in

a trap depends upon the day range of the animal ( $v_i$ ), the number of animals ( $N_i$ ) and the distance at which the trap is triggered ( $D_i$ ). For a given density of animals the number coming into contact with a trap follows a Poisson distribution with mean  $2DN_i$ . Thus equations (2.2c,d) define the off-take.

Finally, equation (2.2e) describes the time allocation constraint, which requires that all available time be allocated between hunting and agriculture.

$$L = L_G + L_S + L_q. \quad (2.2e)$$

When hunting off-takes are non-deterministic, payoffs are defined in terms of expected utilities. We assume throughout that hunters are risk-neutral. The utility maximization problem is based on the notion that households have no property rights in the wildlife that they hunt and therefore have little incentive to take account of the future biological consequences of current decisions. Hence, they are assumed to solve a static optimization problem, taking the time path of variables, such as wildlife stocks, as given.

Equation (2.1) is maximized with respect to  $\gamma_i$  and the labour supply variables ( $L_H, L_S, L_q$ ), subject to the constraints (2.2a)–(2.2e). To illustrate the properties of the model, we reduce the dimensions of the problem and consider the simpler case of two species. This restriction does not alter the qualitative properties of the equilibrium. The first-order conditions are given in electronic Appendix A. By these conditions, households allocate the harvest of each species between consumption and sale, up to the point where the marginal utility from consumption is equal to the foregone net payoffs from the sale of the harvest. Labour is allocated to (say) gun hunting to equalize the net marginal payoffs from gun hunting to the marginal payoffs from agriculture. Hence, the opportunity cost of hunting (by either technique) is defined by the marginal returns to labour allocated to agriculture.

Despite the simple functions adopted, there are no analytical solutions available for the endogenous variables. Hence, to assess the properties of the equilibrium, we derive the general comparative static properties of the first-order conditions (see electronic Appendix A). The impact of changes in the exogenous variables are in general indeterminate, typically because of conflicting income and substitution effects.

There are, however, identifiable situations where the effects can be unambiguously signed. Consider the effect of a rise in the price of (say) species 1. Higher bushmeat prices increase the payoffs from hunting relative to agriculture, so more labour time is devoted to hunting. If, as a result, the harvest of other less valuable species increases sufficiently, then households substitute and consume the lower-valued product (species 2) and sell a greater proportion of the higher-valued product (species 1). This will occur if both the population size and the catchability coefficient for species 2 are relatively large.

We turn next to the labour allocation decisions. Higher bushmeat prices always lead to a shift in labour supply from agriculture to hunting. However, the distribution of labour between snaring and gun hunting is ambiguous. If (say) gun hunting is relatively more efficient at capturing the higher-valued species than snaring, there will be an increase in gun hunting and vice versa. These results are

summarized in the following remark. See electronic Appendix A for proofs.

Result 1: an increase in the price of species  $i$  will: (1) lead to a greater proportion of species  $i$  being sold if the catchability of lower-priced species is sufficiently large; (2) induce an increase in the use of whichever technology is relatively more efficient in capturing species  $i$ .

The effect of an increase in the payoffs from agriculture on all the endogenous variables is ambiguous (electronic Appendix A). Intuitively, an increase in the price of crops raises income and the demand for all goods, including bushmeat. There is therefore a (consumption-driven) incentive to increase the amount of labour time devoted to hunting. However, since the relative payoffs from agriculture are now higher, labour tends to shift to agriculture. It follows that the effects on labour allocation decisions and hence hunting levels are ambiguous. For similar reasons, the impact on household consumption levels is also ambiguous.

Result 2: an increase in the price of agriculture has an ambiguous impact on the proportion of bushmeat consumed and the amount of labour time allocated to each hunting technique.

We turn next to the effect of penalties on harvest decisions. The qualitative impact of raising the expected fine on sold bushmeat is clearly identical in its effects to a reduction in the net price of bushmeat. Hence, the conclusions from Result 1 apply. Raising the expected fine for hunting increases the expected costs of harvesting, which lowers the relative expected payoffs from hunting and hence total amount of labour devoted to hunting. The impact on the distribution of hunting effort between snaring and gun hunting is ambiguous and depends on the interaction between the hunting technology parameters, the intensity of demand for domestically consumed bushmeat and the relative payoffs from sold bushmeat. Similarly, the impact on the proportion of the harvest consumed is also ambiguous.

Result 3: an increase in the expected fine for hunting lowers hunting effort, but has an ambiguous impact on the amount of labour time allocated to each hunting technique and the proportion of the harvest of each species consumed.

### 3. DESCRIPTION OF THE SIMULATION STUDY

The ambiguity of the comparative static results suggests the need for empirical work. Hence, we carried out a simulation of bushmeat hunting in the Ashanti region, Ghana. This is a mixed savannah-forest area with widespread agricultural activity as well as some protected areas of natural vegetation. Bushmeat hunting is common and supplies both local village markets and urban markets (Ntiama-Baidu 1998). Data were obtained from detailed interviews conducted in July 2002 with 85 households in three villages, including 17 hunting households. Key informant estimates and the household survey both suggested that hunters made up 2–4% of the population, coinciding with the results of previous studies (Ntiama-Baidu 1998; Hofmann *et al.* 1999).

Households were asked about their annual revenues from all livelihood activities. Most (89%) of the households farmed, but hunting households were particularly dependent on farming; 73% of the hunting households' non-hunting income was derived from farming compared with

46% in the sample as a whole. Hunters answered detailed questions about the costs of hunting, including fixed and variable costs of the equipment employed and travel costs to market. They also gave information on frequency and length of hunting trips, revenues obtained from sales and agricultural revenues. The hunters partitioned their catch into species eaten at home, given away and sold, and species most frequently caught by each equipment type.

For tractability we focused on five species frequently traded in the urban bushmeat market in Kumasi (making up 68% of open season trade over the period 1987–2002 (D. J. Crookes, E. J. Milner-Gulland and N. Ankudey, unpublished data)). These species were also mentioned as important by hunters in the village surveys, and as being caught by both guns and snares. They are the grasscutter (*Thryonomys swinderianus*), giant rat (*Cricetomys* spp.), bushbuck (*Tragelaphus scriptus*), black duiker (*Cephalophus niger*) and brush-tailed porcupine (*Atherurus Africanus*). We also included two potentially vulnerable species that are only hunted with guns, and also mentioned by hunters in the village surveys: the African civet cat (*Viverra civeta*) and the Mona monkey (*Ceropithecus mona*). The exact choice of species used in the simulations is less important than obtaining a representative spread of life histories, equipment selectivity and protected status.

A discrete time logistic function (Begon *et al.* 1996) was used to describe the biological growth of each species. Thus the net population level of each species is given by:

$$N_{i,t} = \frac{e^{r_i} N_{i,t-1} K_i}{K_i + (e^{r_i} - 1) N_{i,t-1}} - H_{i,t}^G - H_{i,t}^S, \quad (3.1)$$

where  $N_{i,t-1}$  is the population level in period  $t-1$ . The carrying capacity is  $K_i$  and  $r_i$  is the intrinsic growth rate of species  $i$ . These equations were parameterized using allometric relationships (Rowcliffe *et al.* 2003) and information from the literature (see electronic Appendix B). There were no biological data available from the study site.

To assess the impact of bushmeat hunting we combined the model of hunter household behaviour with the biological growth equations to determine the time path of wildlife stocks under alternative scenarios. In the absence of explicit closed form solutions, the model is solved numerically. Thus, the solution to equations (2.1) and (2.2e) defines the household's labour supply and consumption decisions for given wildlife stocks as defined in the allometric equations. The level of hunting emerges from the optimizing decisions and in turn affects wildlife stocks (equation (3.1)), and hunting and consumption decisions the following year. Model parameters were altered to determine the sensitivity of different species to changes in economic circumstances. Electronic Appendix B provides full details of the parameter values, sources of information and estimation methods used to derive certain parameters.

### 4. SIMULATION RESULTS

The benchmark simulation was based on parameter values relating to the current situation in Ashanti. We assume that there is no penalty for harvesting in the benchmark case. The steady-state equilibrium values are given in table 1. All species were above 50% of carrying capacity, varying from 55% (civet cat) to 93% (Mona monkey). This suggests that

Table 1. Equilibrium values for the simulation model with no penalties imposed for hunting. Price rises: all prices increase by a percentage over the benchmark case. (h.p.a., hours per annum.)

price rise	benchmark		+20%		+20%			
	carrying capacity (CC, 100 km <sup>-2</sup> )	numbers (% of CC)	fraction consumed at home	off-take	numbers (% of CC)	fraction consumed at home	off-take	
grasscutter	1 800	1 437 (79%)	0.20	173	868 (48%)	0	275	
giant rat	22 800	19 300 (85%)	0.68	1811	14 900 (65%)	0.57	2 123	
bushbuck	670	448 (67%)	0	38	175 (26%)	0	34	
black duiker	4 300	3375 (78%)	0	56	219 (5%)	0	37	
porcupine	400	280 (72%)	0.39	415	191 (47%)	0.16	421	
Mona monkey	570	531 (93%)	0	220	0	0	0	
civet cat	200	110 (55%)	0.27	8	0	0	0	
gun hunting h p.a.	—	45	—	—	147	—	—	
snaring h p.a.	—	4 964	—	—	12 360	—	—	
welfare level	—	2 723	—	—	2 700	—	—	
price rise	+30%	+30%	+30%	+50%	+50%	+50%	+20%	
species	fraction consumed at home		fraction consumed at home		fraction consumed at home		off-take	
	numbers (% of CC)	off-take	numbers (% of CC)	off-take	numbers (% of CC)	off-take	numbers (% of CC)	off-take
grasscutter	566 (31%)	172	51 (2.8%)	51	0	66	66	
giant rat	10 520 (46%)	3005	2 750 (12%)	2 750	0.08	2 651	2 651	
bushbuck	110 (16%)	21	19 (3%)	19	0	8	8	
black duiker	1 953 (45%)	32	803 (19%)	803	0	17	17	
porcupine	191 (47%)	536	109 (27%)	109	0	518	518	
Mona monkey	0	0	0	0	0	0	0	
civet cat	0	0	0	0	0	0	0	
gun hunting h p.a.	972	—	12 400	12 400	—	—	—	
snaring h p.a.	11 530	—	14	14	—	—	—	
welfare level	2 718	—	2 175	2 175	—	—	—	

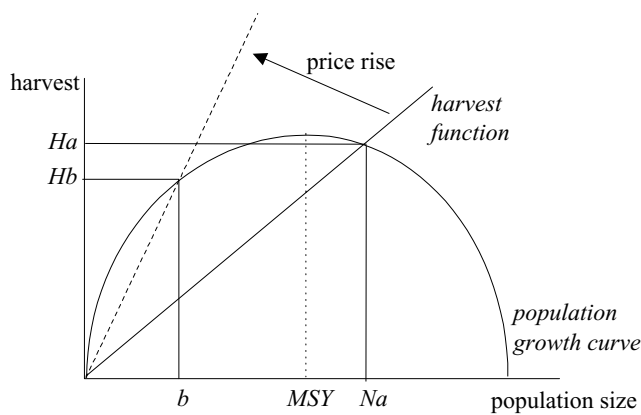


Figure 1. The equilibrium size of an exploited biological stock and the corresponding harvest rate are determined by the point where the harvest function intersects the biological growth curve (e.g. points  $N_a$  = equilibrium population size;  $H_a$  = equilibrium harvest rate). A price rise has the effect of rotating the harvest function to the left (dashed line). Whether this causes harvests to increase or decrease depends on whether the equilibrium moves from one side to the other of the maximum sustainable yield (MSY) point. In the case of the price rise shown, harvest rate is reduced (point  $H_b$ ). Even though we are unable to solve explicitly for the harvest function, it is recognized that it is unlikely to be linear, as shown here. Hence, there are likely to be multiple equilibria—not all of which will be stable. For a useful discussion of these issues see May (1975).

none of the species is over-exploited. Moreover the bulk of hunting effort is devoted to snaring, reflecting the relative costs of the techniques. The survey data indicated that the marginal cost of gun hunting (mainly cartridges) is considerably higher than the marginal cost of snaring (mainly wire). When returns from hunting are low, there is a preference for using (less expensive) snares to harvest bushmeat. Table 1 also summarizes the proportion of each harvested species consumed. In general, lower-valued species (such as giant rats) are more often consumed at home, and this relationship is also complicated by the existence of two hunting technologies.

If the price of all bushmeat is increased by 20%, there is a noticeable reduction in the population of all species, accompanied by an increase in hunting with both snares and guns (table 1). Moreover, civet cats and Mona monkeys are hunted to extinction as a consequence of the increase in gun use. With higher prices there is a stronger incentive to sell a greater proportion of the harvest.

The harvest of some species (e.g. grasscutters and giant rats) increases under higher prices, whereas that of others declines (e.g. bushbucks and black duikers). This is a consequence of the interaction between the equilibrium harvest function (which is increasing in wildlife stocks) and the logistic concave biological growth curve (equation (3.1)). Figure 1 illustrates a possible equilibrium for a single species. A price increase induces an upward movement of the harvest function. If at the new equilibrium the harvest curve intersects the growth curve to the right of the maximum sustainable yield (MSY) point, the harvest will increase, and vice versa. This explains why, for sufficiently small price increases, the harvest of some species rises and that of others declines. The simulations reveal that the

harvest of grasscutters rises by a substantial amount (60%) but that of giant rats by a more modest 18%.

With a 30% and a 50% rise in the price of all species, population levels decline even further. With a 50% price increase the bushbuck and grasscutter populations approach extinction. In this scenario, there is a more extreme switch from snaring to hunting with guns. The population decline is sharp, with equilibrium populations varying from 2.8% of carrying capacity (grasscutters) to 27% of carrying capacity (porcupines). As a consequence, the harvest of all species is lower than in the benchmark case. The simulations therefore reveal that when prices rise sufficiently, adopting the more productive and expensive hunting technique becomes profitable. This switch in technique results in a noticeable decline in wildlife populations. The over-harvesting stimulated by higher prices results in an overall decrease in welfare levels. This is a consequence of the excessive harvesting and depleted resource stocks that typify open access regimes with high prices (Clark 1990).

Since civet cats and Mona monkeys are more vulnerable to extinction than other species, it is useful to assess the impact of a penalty imposed on either the harvest or sale of just these species. For the simulations we assume that bushmeat prices are 30% higher than in the benchmark case. The harvest of civets and Mona monkeys is deemed illegal, and detection results in confiscation of the carcass and a fine of 100 000 cedis (US \$ 11.4). If the penalty is imposed at the point of sale, hunters can avoid it by consuming the protected species at home. Hence, a penalty imposed at the point of sale has a negligible effect on hunter off-takes and welfare, and the two protected species are still extirpated. It is only when a substantial penalty is incurred for hunting the protected species that hunter behaviour changes significantly, towards the benchmark situation of high wildlife stocks, negligible gun hunting and a high proportion of off-take consumed at home (table 2a). A switch from guns to snares occurs only if the aggregate payoffs from hunting fall sufficiently. With a fine that is selectively applied to a subset of species, this calls for a large increase in the expected penalty to induce a switch in hunting techniques. To get a sense of the relative magnitudes involved, a fine of 100 000 cedis and a 20% probability of detection at the point of sale implies that the expected penalty is 20 000 cedis, which is close to the assumed market price of a civet cat in this simulation (23 309 cedis).

We also examine the case in which penalties are imposed across the board for either hunting or sale of bushmeat species. A 20% chance of obtaining a penalty for hunting any bushmeat species has little effect on the outcome, whereas a 20% chance of a penalty on the sale of bushmeat leads to almost complete recovery of wildlife stocks, with off-take being almost exclusively consumed at home. Only very highly priced species are still worth selling (table 2b). Hence the results suggest that imposing penalties on the sale of all bushmeat has a much more profound effect on hunter behaviour, sustainability and welfare than penalties imposed on either hunting or the sale of a subset of species. This is because the sale of bushmeat benefits the household budget, while hunting for home consumption affects the utility from consuming bushmeat (equations (2.1) and (2.2a)). If goods purchased in markets confer higher utility

Table 2a. Equilibrium values for the simulation model with penalties imposed for hunting certain species (civet cats and Mona monkeys) and a 30% increase in bushmeat prices. Detection probabilities are given as per cent for hunting and for sale. (h.p.a., hours per annum.)

detection probabilities	benchmark (no penalty)	0%—hunting 20%—sale	0%—hunting 20%—sale	0%—hunting 20%—sale	15%—hunting 20%—sale	15%—hunting 20%—sale	15%—hunting 20%—sale
species	numbers	numbers (% CC)	fraction consumed at home	off-take	numbers (% CC)	fraction consumed at home	off-take
grasscutter	566 (31%)	594 (33%)	0	108	1 480 (82%)	0.42	96
giant rat	10 520 (46%)	11 220 (47%)	0.39	2500	19 900 (87%)	0.48	1 048
bushbuck	110 (16%)	130 (19%)	0	13	458 (68%)	0.02	12
black duiker	1 953 (45%)	2 088 (48%)	0	20	3 531 (82%)	0	15
porcupine	191 (47%)	193 (48%)	0.17	420	284 (71%)	0.28	261
Mona monkey	0	0	0	0	543 (95%)	0	140
civet cat	0	0	0	0	120 (60%)	0.35	3
gun hunting h p.a.	972	960	—	—	18	—	—
snaring h p.a.	11 530	11 498	—	—	4 965	—	—
welfare level	2 718	2 710	—	—	2 640	—	—

Table 2b. Equilibrium values for the simulation model with penalties imposed either for hunting all species or for selling all species, and a 30% increase in bushmeat prices. Detection probabilities are given as per cent for hunting and for sale. (h.p.a., hours per annum.)

detection probabilities	benchmark (no penalty)	20%—hunting 0%—sale	20%—hunting 0%—sale	20%—hunting 0%—sale	0%—hunting 20%—sale	0%—hunting 20%—sale	0%—hunting 20%—sale
species	numbers	numbers (% CC)	fraction consumed at home	off-take	numbers (% CC)	fraction consumed at home	off-take
grasscutter	566 (31%)	575 (32%)	0	168	1 748 (97%)	0.82	25
giant rat	10 520 (46%)	9 980 (44%)	0.36	3100	22 150 (97%)	1	840
bushbuck	110 (16%)	111 (16%)	0	21	503 (75%)	0.65	9
black duiker	1 953 (45%)	1 966 (45%)	0	29	4 126 (95%)	0.99	6
porcupine	191 (47%)	195 (48%)	0.08	100	380 (93%)	0.61	230
Mona monkey	0	0	0	0	570 (100%)	0	0
civet cat	0	0	0	0	200 (100%)	0	0
gun hunting h p.a.	972	938	—	—	0	—	—
snaring h p.a.	11 530	10 590	—	—	12 500	—	—
welfare level	2 718	2 685	—	—	2 600	—	—

than bushmeat, a large penalty on the sale of *all* bushmeat makes hunting less attractive and hence labour shifts to those activities that generate more fungible forms of income (cash).

Since labour allocated to agriculture defines the opportunity cost of hunting, it is useful to assess whether rising agricultural incomes can be used to curb hunting levels. We examined this possibility for a scenario in which there is a 10% probability of detection and a fine of 100 000 cedis for both sold and consumed meat of the two vulnerable species. Agricultural prices were increased by 25%, 50% and 75% (table 3). The results indicate that total labour time allocated to hunting declines with increased agricultural prices. However, with each consecutive price rise, there is an increase in gun harvesting and a reduction in snaring. Hence, most wildlife populations decline and the two vulnerable species become extinct. The 'technique-switching effect' induced by rising agricultural prices thus negates the beneficial impact of the reduction in labour

time devoted to hunting. Higher agricultural prices raise the opportunity cost of hunting and this makes it more profitable to use the more efficient and expensive hunting technique. This suggests that policies aimed at lowering hunting effort by increasing the payoffs to alternative activities may be less effective in protecting endangered species than direct regulations.

## 5. CONCLUSIONS

Although the importance of bushmeat hunting as a component of livelihoods is widely recognized (e.g. LWAG 2002; Brown 2003), the implications of this have not been explored analytically. The effects of changing the relative profitability of different hunting and non-hunting activities on wildlife populations are not necessarily obvious. In this paper, we have developed a simple modelling approach to the household economy with the aim of providing a firm theoretical foundation for discussions of policy options for managing the bushmeat trade.

Table 3. Equilibrium values with higher crop prices. (h.p.a., hours per annum.)

crop price rise	25%	25%	50%	50%	75%	75%
species	numbers (% CC)	fraction consumed at home	numbers (% CC)	fraction consumed at home	numbers (% CC)	fraction consumed at home
grasscutter	350 (19%)	0	360 (20%)	0	381 (21%)	0
giant rat	7 612 (33%)	0.36	7 016 (31%)	0.33	6 800 (29%)	0.39
bushbuck	98 (15%)	0	111 (16%)	0	109 (15.8%)	0
black duiker	1 638 (38%)	0	1 488 (34%)	0	1 565 (36%)	0
porcupine	172 (43%)	0.09	166 (41%)	0.20	165 (41%)	0.30
Mona monkey	0	0	0	0	0	0
civet cat	0	0	0	0.	0	0
gun hunting h p.a.	2 905	—	5 795	—	5 988	—
snaring h p.a.	9 680	—	5 632	—	5 300	—
welfare level	2 859	—	2 856	—	2 864	—

The general model shows that increases in agricultural prices are ambiguous in their effects on bushmeat hunting because they have the dual effect of increasing the proportion of labour devoted to agriculture rather than hunting, and also increasing the consumption of bushmeat because incomes have risen. Hence, the actual allocation of effort between hunting and agriculture is not clear. This is important because a common suggestion for reducing bushmeat hunting is to invest in agricultural extension (Milner-Gulland *et al.* 2003), which our model suggests may have the unexpected and undesirable side effect of promoting consumption-driven increases in hunting pressure. Even more worrying, our simulations suggest that even when labour devoted to hunting is reduced because of higher agricultural prices, it is likely to become more focused on the more expensive and efficient technology. In our case study, raising agricultural prices actually worsens the conservation status of vulnerable species that are selectively hunted with guns rather than snares.

The general model shows that increases in overall bushmeat prices increase hunting rates. However, given the open access nature of bushmeat this induces overharvesting, depletion of the resource base and consequent resource impoverishment. If restrictions allow species to recover, there is scope for overall welfare gains. The income effect on consumption has been demonstrated empirically by Auzel & Wilkie (2000) for a study site in the Republic of Congo. They showed that the presence of a logging camp increased household bushmeat consumption from 39% of meals in unaffected villages to 49% of meals in villages servicing the logging camp. This was the result of an increase in hunting income caused by the high demand for bushmeat from consumers in the logging camp; logging workers had disposable incomes, and hence 76% of their meals contained bushmeat.

The simulation model shows that increases in bushmeat prices also change the technology used for hunting away from cheaper and less efficient technology (in this case from snares to guns). This has an impact on the species killed, again potentially leading to declines in the more vulnerable species. Whether off-take levels go up or down as hunting effort increases depends on the initial population size (figure 1). The simulations also show that changes in bushmeat prices lead to substantial changes in the proportion of different species consumed at home

rather than being sold on the market. Hence, one finding from our simulations is that there is no need to invoke differential pricing of bushmeat species to explain observed changes in species composition in the market; an overall increase in all prices can also lead to compositional changes. Changes in species composition can reflect changes in species availability, and hence depletion of more vulnerable species (Rowcliffe *et al.* 2003). Here, we show that they can also reflect changes in equipment technology and/or the balance of consumption versus sale of off-take by hunters.

In our simulations, the proportion of grasscutters on sale in the market increased dramatically. This is in line with empirical observations; a market in Kumasi was monitored during a rise in all bushmeat prices, and a substantial increase in the proportion of grasscutters on sale was observed, with all other species remaining relatively stable (D. J. Crookes, E. J. Milner-Gulland and N. Ankudey, unpublished data). Despite this qualitative empirical match, it is not possible to use the Kumasi market data to validate our model more fully, because there is no information available about changes in the proportion of off-take consumed at home, or about the effects of rising prices on the number of new hunters entering the system.

The general model suggests that although penalties reduce hunter effort, they have an ambiguous effect on the distribution of effort between technologies and on consumption versus sale of off-take. In the simulations, we examined the effects of detection while hunting and at the point of sale separately. This has policy relevance because it has been proposed that restrictions on protected species should be strongly enforced, while allowing legal hunting on more resilient species to continue. This is suggested as a way to enable participants in the bushmeat trade to receive much the same welfare benefits as previously, while reducing pressure on vulnerable species (Milner-Gulland *et al.* 2003).

We started by using the currently legislated fine for hunting protected species in Ghana, 10 000 cedis (US \$ 1.14), but unsurprisingly this fine had no effect. A fine rate of 100 000 cedis on the two vulnerable species had an effect only if detection probabilities at the point of sale were high. The effect is to cause a switch away from gun-hunting, which leads to an increase in the population size of all species, not just the protected species. The simulations suggest, therefore, that targeted law enforcement, based on the most vulnerable species, is likely to have wider-ranging

effects than might have been anticipated, if it is reducing hunters' abilities to use efficient technology because of the non-selective nature of hunting. The results also suggest that the current fine level is insufficient to have any effect on hunter behaviour or off-take rates; this is as observed in empirical studies; for example Ntiamao-Baidu (1998) found protected species on sale during the closed season.

In this study, we developed a simple general model of the household economy as a way of placing bushmeat hunting into the wider context of individual decision-making. This is a first step towards understanding how conservation and development policies might affect hunter behaviour, and hence both the conservation status of species and welfare of participants in the bushmeat trade. It highlights the importance of considering links between agriculture and hunting when developing conservation policies. This work now needs to be integrated with detailed empirical studies of the bushmeat trade, to produce a more rounded understanding of the factors underlying the 'bushmeat crisis'.

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## REFERENCES

- Auzel, P. & Wilkie, D. 2000 Wildlife use in northern Congo: hunting in a commercial logging concession. In *Hunting for sustainability in tropical forests* (ed. E. L. Robinson & J. R. Bennett), pp. 413–426. NY: Columbia University Press.
- Bakarr, M. I., da Fonseca, G. A. B., Mittermeier, R., Rylands, A. B. & Painemilla, K. W. (eds) 2001 *Hunting and bushmeat utilization in the African rain forest*. Advances in Applied Biodiversity Science Number 2.
- Barrett, C. B. & Arcese, P. 1998 Wildlife harvesting in integrated conservation and development projects: linking harvest to household demand, agricultural production and environmental shocks in the Serengeti. *Land Economics* **74**, 449–65.
- Begon, M., Mortimer, M. & Thompson, D. J. 1996 *Population ecology: a unified study of animals and plants*, 3rd edn. Oxford: Blackwell Science.
- Bennett, E. L. 2002 Is there a link between wild meat and food security? *Conserv. Biol.* **16**, 590–592.
- Brown, D. 2003 *Bushmeat and poverty alleviation: implications for development policy*. ODI Wildlife Policy Briefing Number 2. Overseas Development Institute, London.
- Clark, C. W. 1990 *Mathematical bioeconomics: the optimal management of renewable resources*, 2nd edn. NY: Wiley-Interscience.
- Cowlisshaw, G. C., Mendelson, S. & Rowcliffe, J. M. 2005 Market structure and trade in a bushmeat commodity chain. *Conserv. Biol.* (In the press.)
- Damania, R., Stringer, R., Karanth, K. U. & Stith, B. 2003 The economics of protecting tiger populations: linking household behavior to poaching and prey depletion. *Land Economics* **79**, 198–215.
- de Merode, E., Homewood, K. & Cowlisshaw, G. 2004 The value of bushmeat and other wild foods to rural households living in extreme poverty in Democratic Republic of Congo. *Biol. Conserv.* **118**, 573–581.
- Fa, J. E., Currie, D. & Meeuwig, J. 2003 Bushmeat and food security in the Congo basin: linkages between wildlife and people's future. *Environ. Conserv.* **30**, 71–78.
- Glenn, M. 2003 *Guenons diversity and adaptations in African monkeys*. Amsterdam: Kluwer.
- Hill, K. & Padwe, J. 2000 Sustainability of Aché hunting in the Mbaracayu Reserve, Paraguay. In *Hunting for sustainability in tropical forests* (ed. J. R. Robinson & E. L. Bennett), pp. 79–105. NY: Columbia University Press.
- Hofmann, T., Ellenberg, H. & Roth, H. 1999. *Bushmeat: a natural resource of the moist forest regions of West Africa with particular consideration of two duiker species in Côte d'Ivoire and Ghana*. TöB Publication number TöB F-V/7e. Eschborn, Germany: GTZ.
- LWAG 2002 *Wildlife and poverty study*. Livestock and Wildlife Advisory Group. London: UK Department for International Development.
- May, R. 1975 *Stability and complexity in model ecosystems*. Princeton University Press.
- Mendelson, S., Cowlisshaw, G. & Rowcliffe, J. M. 2003 Anatomy of a bushmeat commodity chain in Takoradi, Ghana. *J. Peasant Studies* **31**, 73–100.
- Milner-Gulland, E. J. & Bennett, E. L. (and the SCB 2002 Annual Conference Wild Meat Group). 2003 Wild meat—the bigger picture. *Trends Ecol. Evol.* **18**, 351–357.
- Ntiamao-Baidu, Y. 1998 *Wildlife development plan*. vol. 6. Sustainable harvesting, production and use of bushmeat. Wildlife Department: Accra, Ghana.
- OIA 2000 *Microlivestock*. Washington DC: Office of International Affairs, National Academies Press.
- Robinson, J. R. & Bennett, E. L. 2000 *Hunting for sustainability in tropical forests*. NY: Columbia University Press.
- Rowcliffe, J. M., Cowlisshaw, G. C. & Long, J. 2003 A model of human hunting impacts in multi-prey communities. *J. Appl. Ecol.* **40**, 872–889.

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