Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions

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Legislation for the protection of species is a global conservation tool. However, in many developing countries lack of resources means that effectiveness relies on voluntary compliance, leading to contradictory assumptions. On one hand, laws introduced without effective enforcement mechanisms carry an implicit assumption that voluntary compliance will occur. On the other hand, it is often openly assumed that, without enforcement, there will in fact be no compliance. Which assumption holds has rarely been rigorously tested. Here we show that laws for the protection of some species of large mammal have no effect on the prey choice patterns of primarily commercial hunters in the Democratic Republic of Congo, confirming the second assumption. We established this result by using an optimal diet model to predict the pattern of prey choice in the absence of regulation. Prey choice patterns predicted by the model were accurate across a range of conditions defined by time, space and type of hunting weapon. Given that hunters will not comply voluntarily, the protection of vulnerable species can only take place through effective enforcement, for example by wildlife authorities restricting access to protected areas, or by traditional authorities restricting the sale of protected species in local markets.

Keywords: bushmeat; wildlife law enforcement; human hunters; optimum diet model

1. INTRODUCTION

Species conservation is typically implemented either through the designation of protected areas or through regulations to protect vulnerable or important species. However, in the developing world, resource constraints greatly limit the ability of governments to implement conservation legislation (Wilkie *et al.* 1992; Peres & Terborgh 1995; Wilkie *et al.* 2001). In effect, this means that laws are often implemented with little or no enforcement to back them up, requiring an implicit assumption that resource users will voluntarily modify their behaviour in accordance with the law. In the case of protected area legislation, the available evidence is largely against this assumption, with levels of illegal resource use (Leader-Williams *et al.* 1990; Milner-Gulland & Leader-Williams 1992; Leader-Williams & Milner-Gulland 1993; Abbot & Mace 1999) and rates of decline in exploited populations (Leader-Williams & Albon 1988) both having been shown to respond strongly to patrol effort in protected areas. There is also some evidence that the rate of offtake of protected species outside protected areas declines with increasing enforcement effort (Milner-Gulland & Clayton 2002). However, the effectiveness of species protection laws in the absence of enforcement has not previously been systematically assessed. We addressed this issue in a region of central Africa where limited hunting is allowed, but where the law prohibits the hunting of some mammal species. Specifically, we test the hypothesis that legal protection influences the likelihood that hunters will target unprotected species in preference to protected species.

We used data on the behaviour of hunters while hunting, revealing whether any given encounter with prey led to its pursuit. This kind of information gives us a more powerful test of the above hypothesis than the presence or absence of bushmeat species in local markets or diets, for two reasons. First, if there is a small risk that ignoring protected status could lead to prosecution or harassment, capture of protected species may be prevalent but concealed, making it difficult to detect away from the hunting grounds. Second, protection that is partly effective, thus reducing the rate of capture of protected species rather than eliminating it entirely, cannot be detected without knowing what rate of capture would be expected in the absence of protection. This can only be estimated when there is information on the rate at which hunters encounter these species.

There is a further complication, in that failure to pursue a given species may have nothing to do with its protection status, but may instead be driven by the hunters' own preferences. We therefore need to control for any such preferences if we are to be sure that a given pattern of behaviour is influenced by protection status. In other words, in order to demonstrate whether protection reduces the likelihood of attack, we need to know what the expected likelihood would be in the absence of protection.

One way to assess the expected likelihood of attack in the absence of protection would be to gather baseline information before the imposition of protection laws, before carrying out the study. However, this degree of foresight is rarely possible. An alternative, and the approach taken here, is to use a model of hunter behaviour that can give us the predicted likelihood of attack across a range of species. This assumes optimal behaviour that is uninfluenced by any external force, such as the risk of penalties for catching

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certain species, and can therefore potentially provide baseline predictions against which the observed pattern of choice can be tested. Optimal prey choice models have been developed and tested, in many cases successfully, for a wide range of animal foragers (Sih & Christensen 2001). They have also been successfully applied to human hunters (Hawkes *et al.* 1982; Kuchikura 1988; Smith 1991; Alvard 1993), but thus far only in subsistence hunter-gatherer societies; the relevance of prey choice models to human hunters operating in a primarily commercial environment has not previously been tested.

Here we test the reliability of a prey choice model when applied to commercial hunters in the Democratic Republic of Congo (DRC), and use the model's predictions as a baseline against which to test the hypothesis that species protection status influences the prey choice patterns of hunters. Data were collected during a period of civil conflict and during the preceding period of peace, from hunters operating illegally within a protected area (Garamba National Park) and those operating legally in a hunting reserve, and from hunters using either shotguns or rifles. We predicted that during the period of conflict, breakdown of civil society would lead to a relaxation of any controls on hunter behaviour that may previously have existed. With regard to location, hunters operating in the protected area were ignoring regulations simply by going there, so we predicted that their prey choice patterns would be less likely to take account of species protection rules than those of hunters in the hunting reserve. Similarly, since hunters using automatic rifles are acting illegally simply by possessing these weapons, we would expect their prey choices to be less influenced by species protection status than that of shotgun hunters. In each example, we would expect the case with less compliance to show more closely optimal prey choice than the case with more compliance. These predictions thus provide us with a means to refine our test of the hypothesis set out above.

2. MATERIAL AND METHODS

The methods used to collect data on hunting were designed according to the specific hunting practices observed at Kiliwa and Mamba, two villages in the Azande Hunting Reserve, northeast DRC (de Merode 1998). Mamba is located less than 10 km from Garamba National Park, and hunters from this village regularly hunted inside the Park. Kiliwa is about 40 km from the National Park, and hunters from here operated entirely within the hunting reserve. These communities are made up primarily of Azande subsistence agriculturalists, with smaller numbers of Logo and Mondo migrants from the east. The Zande economy is predominantly agricultural, but, as in most central African rural cultures, their modes of subsistence extend into the surrounding wild lands through hunting, fishing and gathering (de Schlippé 1954; Evans-Pritchard 1971).

Information was obtained during 1996 and 1997 from 27 hunters, over 189 hunts, totalling 568 hunting hours, during which there were 1111 encounters with potential prey, covering 33 species (31 mammals and 2 birds). Care was taken to monitor an equal number of hunts from each of the hunters in order to avoid a bias towards the results of any particular individual. This was achieved by selecting hunters from a complete list of those undertaking various types of hunting that was established as part of a village survey prior to the hunting study (de Merode *et al.* 2004).

For each hunt, total time hunting was recorded as the period during which the hunter was actively seeking animals to shoot. The start of the hunt was marked by the hunter preparing the gun, while the end was marked by the hunter stating when the hunt was over. Stalking time was recorded as the time from when an animal was first detected to the point at which either the hunt was abandoned or the carcass was retrieved. All encounters with potential prey species were recorded, together with the outcome of the encounter, specifically whether they were stalked, and if so, whether the stalk ended in one or more animals being killed. Finally, the weights of carcasses were recorded.

In the case of shotgun hunts, the above data were monitored directly. Permission to join the hunts was solicited from the hunters, who were consulted several days beforehand in order to agree on a date and time for the researcher to join a hunt. However, it was not possible to participate in hunts involving automatic rifles because the unauthorized possession of automatic weapons in Congo is a criminal offence. As a consequence, data on rifle hunts were collected by interviewing the hunters immediately on their return from a hunt, recording the hunters' own recollections of encounters, actions and timings, and weighing the carcasses brought home.

For predicting expected prey choice patterns, we used a classic optimal diet model (Pulliam 1974; Charnov 1976). The basis of this model is that prey types (in this case species) are added to the chosen set in descending order of profitability, F , until the profitability of the next type is less than the current cumulative gain rate, G , including the i th type and all those more profitable:

$$F_{i+1} < G_i.$$

Prey type $i + 1$ and all less profitable types are then excluded from the chosen set. This can be intuitively understood by seeing that the overall gain rate would be reduced by adding this next prey type. Profitability is defined as the total value gained per unit handling time:

$$F_i = q_i V_i / H_i,$$

where V is the value of an individual animal, q is the number of individuals killed per prey group, and H is the handling time per prey group. The gain rate is defined as the cumulative value obtained, divided by the total cumulative time spent searching for and handling this catch:

$$G_i = \sum_{j=1}^i V_j q_j E_j / \left(1 + \sum_{j=1}^i H_j E_j \right),$$

where E is encounter rate.

Hunters were frequently accompanied by assistants who, in the event of a large animal being killed, processed the carcass and transported the meat, in return for a share of the meat. Furthermore, the monetary value of meat per unit weight did not differ between species (de Merode 1998). Species value, V , could therefore be quantified as the average carcass weight, reduced by the average amount of meat given in payment. For 12 of the 33 species recorded, no carcass or payment weights were obtained. In these cases, value was given by average body mass, as reported elsewhere (Silva & Downing 1995), minus the expected average payment based on the observed relationship between payment and body mass. The number of individuals killed per group, q , was calculated as the total number of individuals of a given species that were killed divided by the number of encounters with that species in which at least one kill was made.

Handling time was defined as the time required to make a kill (including time wasted in unsuccessful attempts). Time costs for

processing and transporting carcasses were ignored because they were either negligible (in the case of smaller species) or borne by assistants in return for payment, rather than by the hunter himself (in the case of larger species). Handling times varied between species, between locations and between weapon types, so specific H values were calculated as the average handling time for each of these category combinations. Where there were insufficient data to derive a direct handling time estimate for a given combination, a value was interpolated using the fitted value from a statistical model of $\log_e$ handling time in relation to each of the factors listed above.

Encounter rate, E , is defined as the number of successful kills per unit search time. Because not all encounters were pursued, and for some species no successful kills were recorded, it is necessary to calculate encounter rate indirectly as

$$E = kN_E/T,$$

where N_E is the number of encounters (whether ignored or pursued), k is the probability that a pursuit will lead to a kill, and T is the search time (total hunt time minus time spent travelling and handling). For species in which a large number of kills were observed, the probability of a kill was calculated directly as the number of kills observed divided by the number of pursuits initiated. Across all species, k was not affected by weapon type, but did increase with increasing body mass. Fitted values from this statistical model were used to predict k values for species in which too few kills were recorded to calculate k directly. More detailed discussion of the issues involved in the parameterization of the prey choice model for human hunters can be found in Rowcliffe *et al.* (2003).

Probability of attack was analysed using generalized linear mixed models with binomial errors, implemented in MLwiN 1.10 (Rasbash *et al.* 2000). We fitted hunter, hunt, species and observation as random effects, prior to adding the explanatory variables (fixed effects), thus taking account of the structure of our data, which included repeated observations within the random effects (see Goldstein 2003 for the rationale of using such models). In this data set, observations were nested within hunts within hunters, while species were cross-classified with hunts and hunters (i.e. a given species could be encountered by more than one hunter on more than one hunt).

3. RESULTS

(a) Testing the prey choice model

Figure 1 shows the observed patterns of attack behaviour with the actions predicted by the prey choice model for eight different cases separated by location, period and weapon type. In all cases, the predictions fell close to the observed inflection points of the logistic curves fitted to the data. The accuracy of these predictions is summarized across all the graphs in figure 1 by plotting the observed inflection points against the predicted threshold profitability values (figure 2). This emphasizes the overall goodness of fit between predicted and observed, but also shows some other interesting patterns. First, the profitability threshold was much lower among shotgun hunters than among rifle hunters ($\chi^2_1 = 60.9$, $p < 0.0001$), a result of the fact that very large species (elephant, buffalo and hippo) are not vulnerable to attack by shotgun hunters. Without these large species, it is profitable for shotgun hunters to accept a broad range of species with body masses down to a few kilograms, in contrast to rifle hunters, who ignore most species with a body mass much below 100 kg. Second, the

Figure 1. Probability of pursuit in relation to species profitability (biomass gained per unit handling time). Each point represents the proportion of encounters that were attacked for a given species. Curved lines represent the best-fit logistic regressions of encounter response (pursue or ignore) in relation to profitability. Note that species points are derived from a variable number of encounters, so have varying weights in the regressions. The vertical lines represent the threshold profitability values derived from the prey choice model, above which species are predicted to be attacked, and below which they are predicted to be ignored. Relationships are shown for all eight combinations of location (Kiliwa/Mamba), period (war/peace) and weapon type (rifle/shotgun).

profitability threshold was higher in Mamba ($\chi^2_1 = 16.9$, $p < 0.0001$). This effect can be ascribed to a greater abundance of game in this area resulting from its proximity to the National Park. Finally, while there was no overall effect of period ($\chi^2_1 = 0.58$, $p > 0.4$), the profitability threshold was higher during wartime among rifle hunters ($\chi^2_1 = 4.28$, $p < 0.05$) and in Mamba (although this effect was not statistically significant: $\chi^2_1 = 2.53$, $p > 0.1$). These effects can be explained by the fact that controls on hunting in the protected area broke down during the conflict, thus increasing access by rifle hunters to areas with abundant large game (de Merode 1998).

Encounters with species that were predicted to be unprofitable were ignored in 82% of cases, and encounters with species that were predicted to be profitable were pursued in 76% of cases (figure 3a). Overall, the accuracy of the prey choice model prediction was 79%. Deviations

Figure 2. Observed profitability threshold separating generally pursued species from those generally ignored plotted against profitability threshold predicted by the prey choice model. The observed thresholds were given by the inflection points of the logistic regressions fitted to the data, illustrated in figure 1.

Figure 3. Proportion of encounters that resulted in attack, separated by whether the prey choice model predicted pursuit or not: (a) all data combined; (b) data separated by species protection status. Figures over bars give the total numbers of encounters in each category.

from predictions were most frequent close to the threshold profitability values; this effect is visible in figure 1, and was highly significant (probability of correct prediction in relation to distance from threshold: $\chi^2_1 = 137$, $p < 0.0001$).

(b) Testing the influence of wildlife law

If legal protection were to any degree effective, we would predict that the proportion of encounters with protected species that were pursued would be lower than the baseline case in figure 3a, especially for species predicted to be unprofitable. Conversely, given that some profitable encounters would be ignored, we would expect encounters with unprotected species to become more likely to be pursued than in the baseline case, particularly encounters with species predicted to be profitable. In fact, this predicted pattern was not observed (figure 3b). Indeed, among protected species, the probability of pursuit was *greater* than the baseline case, both in species predicted to be pursued and in those predicted to be ignored. Among unprotected species, the pattern was virtually the same as in the baseline case. Controlling for predicted action, protected species were significantly more likely to be attacked than unprotected species ($\chi^2_1 = 7.8$, $p < 0.01$).

This apparently perverse result is in fact not a causal association, but rather an artefact of the positive association between protected status and profitability (figure 4). Species that are protected also tend to be larger and more profitable, and are therefore much more likely to fall close to the profitability threshold (in the case of species predicted to be ignored), or well above it (in the case of species predicted to be pursued). Given that the degree of deviation from predictions decreases with increasing distance from the threshold profitability, this results in a greater apparent probability of pursuit of protected species, regardless of the predicted action. This was confirmed by analysis of attack probability in relation to status, controlling for profitability relative to the predicted threshold ($\ln[F/\theta]$, where F is profitability and θ is predicted threshold). This variable controls both for model prediction, as in the previous test, and for proximity to the profitability threshold. In this case, protected status had no significant effect on the probability of attack ($\chi^2_1 = 1.07$, $p > 0.25$).

The summary conclusion from these results is that legal protection has had no effect on hunters' prey choice decisions in this system. However, it may be that protection is effective in some cases but not others—either at certain times, in certain places, or among particular groups of hunters. We examined this possibility by testing the significance of interaction between protection status and either place, period or weapon type, controlling for profitability relative to the predicted acceptance threshold. This indicated that there was no significant deviation from predicted optimal behaviour in different periods ($\chi^2_1 < 0.01$, $p > 0.9$) or in different places ($\chi^2_1 = 2.51$, $p > 0.1$). Our hypotheses that law-abiding behaviour should be least apparent during wartime, or among hunters operating from Mamba, were not therefore supported. However, there was a significant interaction between weapon type and protected status. While shotgun hunters did not show any significant deviation from predicted optimal responses ($\chi^2_1 = 0.24$, $p > 0.5$), rifle hunters were more likely than expected to attack protected species of a given relative profitability ($\chi^2_1 = 20.5$, $p < 0.0001$). This does not support our prediction that shotgun hunters would be more likely to make suboptimal prey choices by avoiding protected species, whereas rifle hunters would be more likely to ignore species status and make optimal prey choices. While this appears to indicate a failure of the optimality model, the increased probability of attacking protected species among rifle hunters is driven by only 28 encounters in which an attack took place when it was predicted to be suboptimal. Of these, 20 encounters were with a single species (red river hog *Potamochoerus porcus*). The most likely explanation for this departure from expected choice is therefore that profitability was underestimated for this species. For example, the rifle-specific handling time estimate for this species was relatively high (22 min, compared with an average across species of 17 min), and reducing the handling time to the cross-species average was sufficient to increase profitability above the optimal threshold. It therefore seems likely that relatively minor inaccuracies in parameterization, together with a relatively small unbalanced sample, could explain the apparently perverse response of rifle hunters to protected species.

Figure 4. Species profitabilities in rank order, with protection status indicated for each. Species codes: 1, cane rat *Thryonomys* spp.; 2, mongoose *Herpestes*, *Mungos* and *Dologale* spp.; 3, palmnut vulture *Gypohierax angolensis*; 4, helmeted guinea fowl *Numida meleagris*; 5, aardvark *Orycteropus afer*; 6, blue duiker *Cephalophus monticola*; 7, Dent's monkey *Cercopithecus denti*; 8, agile mangabey *Cercocebus agilis*; 9, patas monkey *Cercopithecus patas*; 10, Uganda grass-hare *Poelagus marjorita*; 11, red-tailed monkey *Cercopithecus ascanius*; 12, chimpanzee *Pan troglodytes*; 13, tantalus monkey *Cercopithecus tantalus*; 14, de Brazza's monkey *Cercopithecus neglectus*; 15, bush duiker *Sylvicapra grimmia*; 16, crested porcupine *Hystrix cristata*; 17, guereza colobus *Colobus guereza*; 18, red duikers *Cephalophus rufilatus* and *dorsalis*; 19, sitatunga *Tragelaphus spekei*; 20, common warthog *Phacochoerus africanus*; 21, olive baboon *Papio anubis*; 22, red river hog *Potamochoerus porcus*; 23, bushbuck *Tragelaphus scriptus*; 24, giant hog *Hylochoerus meinertzhageni*; 25, African civet *Civettictis civetta*; 26, kob *Kobus kob*; 27, bohor reedbuck *Redunca redunca*; 28, hartebeest *Alcelaphus buselaphus*; 29, bongo *Tragelaphus euryceros*; 30, waterbuck *Kobus ellipsiprymnus*; 31, African buffalo *Syncerus caffer*; 32, elephant *Loxodonta africana*; 33, hippopotamus *Hippopotamus amphibius*.

4. DISCUSSION

Broad agreement between a simple diet choice model and prey choice observations has previously been reported in a number of subsistence hunting societies (Hawkes *et al.* 1982; Kuchikura 1988; Smith 1991; Alvard 1993), despite the fact that prey choice in such societies is likely to be heavily influenced by cultural factors as well as simple maximization of gain rate (Hawkes 1990; Hawkes 1991). The system described here differs from any previous test of the optimal diet model in humans of which we are aware, in that the hunting is overwhelmingly commercial in nature, being targeted at the supply of meat for sale in local village and urban markets (de Merode *et al.* 2004). We might expect such a system to be, if anything, less likely to be prone to cultural taboos or preferences than in subsistence hunter-gatherer societies, and therefore more likely to be

ruled by simple optimality decisions. This conclusion is supported by the ability of the model to predict shifts in the optimal prey set associated with different weapon types, locations and periods. In one of six possible tests (rifle hunters), the model appeared to fail in a way that was not consistent with compliance with protection laws. However, we believe that this reflects problems with parameterization associated with a small, unbalanced sample rather than a structural failure of the model.

The data did not show the 'all or nothing' shift from acceptance to rejection predicted by the model, but such partial preferences are to be expected in data obtained by observation without experimental control of conditions (McNamara & Houston 1987). In fact, partial preference theory predicts that uncertainty in behaviour should be greatest around the predicted threshold profitability level (McNamara & Houston 1987), and this pattern was observed.

The second major conclusion of this study is that there is no evidence for the effectiveness of wildlife protection laws aimed at preventing the exploitation of vulnerable species. This is perhaps not surprising, given the minimal enforcement of species protection laws at any time or in any location during this study. Even during peacetime, when overall hunting effort in nearby Garamba National Park was effectively constrained by park patrols and market institutions (de Merode 1998), there was no evidence that prey choice was influenced by species protection laws.

This is a dispiriting conclusion, given that the rational sustainable exploitation of wild meat ideally depends on the ability to control selectively the offtake of different species. The extraction of bushmeat cannot be halted entirely; neither should this be considered a desirable goal outside protected areas, on the basis that many households living in extreme poverty are highly dependent on bushmeat for food and income (DFID 2002). This conflict of interest between conservation and human development could potentially be solved by allowing the exploitation of abundant, highly productive species that are resistant to exploitation, while protecting the more vulnerable species (G. Cowlishaw, S. Mendelson and J. M. Rowcliffe, unpublished data). Unfortunately, as the results of this study have shown, such selective protection is likely to be extremely difficult to achieve.

Sanctions for the taking of protected species were not imposed over most of the surveyed area during this study. On this basis, as well as on theoretical grounds (Milner-Gulland & Leader-Williams 1992), the effectiveness of species protection laws could be improved most dramatically by increasing the probability that violations will be detected, rather than by increasing penalties. In wealthier countries, where game management is largely privately controlled and can be supported by high levels of dedicated manpower, enforcement is effectively achieved through a combination of private and state policing. Policing is not impossible in countries such as the DRC, but mechanisms for obtaining sufficient and sustainable funding are necessary if law enforcement is to be effective (Jachmann & Biliouw 1997). Complementary approaches, drawing on the capacity of traditional administrations to restrict access to markets and technology, are also being tested and have provided encouraging results (de Merode 2004). This points to the engagement of such community-based

authorities in the enforcement of selective species protection laws as a promising avenue for progress.

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