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Overcoming extinction: understanding processes of recovery of the Tibetan antelope

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Abstract. Since the middle of the 20th century, the Tibetan antelope (*Pantholops hodgsonii*) has been poached for its wool to make luxury shawls, *shahtoosh*. This direct overexploitation caused a drastic decline in their population, with a loss of more than 90% compared to the baseline population a few decades ago. Assuming this is an anthropogenic Allee effect (AAE), human attraction for rarity can drive rare species to extinction, which could explain the increasing rates of antelope harvests, paralleling the escalating prices of *shahtoosh* as the species got rarer. Since 1999, international concern led to conservation actions and the population soon started increasing. This unique situation allowed the presence of an AAE in Tibetan antelope to be tested, as well as an assessment of the potential effects of conservation actions in the presence of this process. We developed a theoretical discrete-time population dynamics model and examined effects of variation in *shahtoosh* prices. Furthermore, we tested the effects of major conservation actions into our models assessing their relative contribution to population recovery. During the exploitation phase, we found some evidence supporting the presence of an AAE compared to non-AAE models when hunting ceased at antelope population sizes below 10% of the initial population size. Regarding the conservation phase, our results suggested that poacher numbers reduction had the most likely positive impact on Tibetan antelope population dynamics. As many other species are similarly declining and/or close to extinction, our results suggest that adequate conservation actions could counter the most dramatic declines, even when populations have entered an extinction vortex.

Key words: anthropogenic Allee effect; conservation actions; luxury products; *Pantholops hodgsonii*; poaching; population dynamics; *shahtoosh*; Tibetan antelope.

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Introduction

Overexploitation of species including consumption for food and medicines has become one of the most important threats to the survival of many taxonomic groups (Peres 2010). In most cases, the primary motivation for wildlife exploitation is economic. This has led to the rapid expansion of wild animal exploitation, trade and especially illegal trafficking (Zhang et al. 2008). The global trade in illegal wildlife is a multi-billion dollar business and is now the second-largest black market worldwide (Toledo et al. 2012). Species concerned by illegal trade are numerous, as are their geographic origins, but most seizures occur in Southeast Asia and particularly in China (Li et al. 2000, Rosen and Smith 2010). Unsustainable trade has been identified as one of the main conservation challenges in this region (Nijman 2010).

China is also a major market for luxury wildlife products (Corlett 2007). This fast-growing market raises pressure on many wildlife species, with potentially irreversible consequences for many. The trade of luxury goods is one of the human activities that can lead to an anthropogenic Allee effect (AAE). It occurs in economic markets of wildlife trade in which humans attribute an excessive value to rarity and thus disproportionately exploit rare species, thereby making them even rarer, and ultimately precipitating their extinction (Courchamp et al. 2006). Where traditional economic theory suggests that rare species suffer less exploitation because of high exploitation costs (Clark 1990), the AAE theory claims that these high costs can be met by high prices for rare species. When a species is valued for its rarity, customers continuously adjust their willingness to pay more, thus maintaining trade profitability. Consequently, its exploitation may continue, leading the species into an extinction vortex (Hall et al. 2008).

One example of a luxury wildlife product market is the worldwide demand for *shahtoosh* shawls made from the wool of the endemic ungulate Tibetan antelope (*Pantholops hodgsonii*) (Harris et al. 1999). The under-wool of this species is considered as the finest wool in the world. To produce a single shawl, poachers need to kill between three and five antelopes (Wright and Kumar 1997). The increase of *shahtoosh* product demand during the late 20th century caused both a drastic increase of their market price and an increase in pressure (IFAW/WTI 2001), leading to a dramatic decline of the Tibetan antelope population (Schaller 1993). In the early 1990s, this species was at a critically low population size, declining by 90% relative to 1950 (Schaller 1998). Illegal overexploitation of Tibetan antelope for *shahtoosh* wool has contributed to the slaughter of thousands of antelopes over decades. In 1975, this species was listed as an Appendix II species (CITES), and was moved to Appendix I four years later, thus obtaining the highest legal protection (Ginsberg and Schaller 1999). Despite this protection, Tibetan antelope was categorized as endangered in 2000 by the International Union for Conservation of Nature (IUCN). In 1999, an International Workshop on the Conservation and Control of Trade in Tibetan antelope, held in Xining (China), promoted international cooperation to implement conservation actions to stop illegal hunting (Liang and Schwabach 2007). In 2003, the estimation of Tibetan antelope population size reached the minimum number of 50,000 individuals (Appendix: Table A1). Since then, Tibetan antelope populations have started recovering, with about 200,000 individuals currently (Antelope Specialist Group 2011). However, no studies have assessed theoretically the drivers that led to its population decline and then recovery, even though assessments of conservation measures have been important over the last decade for other emblematic species like the black or white rhinoceroses (Brodie et al. 2011, Ferreira et al. 2012).

We explored and predicted the population dynamics of Tibetan antelope during two phases of exploitation and conservation using empirical data coupled with theoretical mathematical models. Specifically, we tested whether the presence of an AAE in the Tibetan antelope population could have precipitated its decline through overexploitation. We developed a discrete-time model that describes the theoretical population dynamics of this species with and without AAE and assessed which model best fits available data for the exploitation phase. Secondly, we modeled four theoretical conservation scenarios (i.e., poacher numbers reduction, catchability reduction, poaching cost increase, and all three actions simultaneously) to assess their theoretical effects on population size trajectories.

Materials and Methods

Study species

The Tibetan antelope is the only genus of large endemic mammals of the Tibetan plateau located both in China and India (Leslie and Schaller 2008) and endures one of the harshest environments on earth, where extreme temperatures can fall as low as −40°C (IFAW/WTI 2001). The Tibetan antelope is a herbivorous ruminant and mixed feeder (Leslie and Schaller 2008) which is gregarious. A large part of its population is migratory, but both sexes live separately for most of the year, coming together during the winter rut (Schaller 1998).

Accurate density data of Tibetan antelope are difficult to obtain because of the vast area of the Tibetan Plateau, variable intersexual herding behavior, movements (migratory or resident), and spatial use over time (calving areas; Leslie and Schaller 2008). Despite this, various sources have provided estimations of Tibetan antelope population sizes in the literature. We collected their population size data from the International Union for Conservation of Nature (IUCN) and from other published studies for different years (Appendix: Table A1). To our knowledge, these population size data represent the most comprehensive data available.

AAE assumptions

One fundamental process, which generates an AAE, is the presence of a positive correlation between species rarity and its value (Courchamp et al. 2006 for details). We explored the relationship between Tibetan antelope population size and *shahtoosh* shawl price (N = 7), inflation corrected by the 2006 rate (BLS 2006), as a proxy of Tibetan antelope rarity and value, respectively (Appendix: Tables A1 and A2).

Theoretical models of Tibetan antelope population dynamics

The core model for Tibetan antelope population dynamics consisted of standard Verhulst discrete-time models (Verhulst 1838). We included a poaching pressure model, which is reproduced by the Gordon-Schaefer production function (Gordon 1954) (Eq. 1):

$$N_{t+1} = N_t + r_m N_t \left(1 - \frac{N_t}{K}\right) - q \times E \times N_t \qquad (1)$$

where r_m is the growth rate, K the carrying capacity, N_t the population size at time t, q the catchability of the species, E the hunting effort, and $(q \times E \times N_t)$ is the Gordon-Schaefer production function.

Then we replaced fixed hunting effort (E) in Eq. 1 by a dynamical function for hunting effort (E_t) following the recommendations of Hall et al. (2008). Using this equation, we assumed that rare species are harvested at a rate depending both on the price and cost associated with hunting effort. Changes in hunting effort were assumed to be proportional to changes in profit, which is the difference between the price obtained for the harvest and the total cost associated with the hunting effort (Eq. 2) (Hall et al. 2008). This gives the following Eq. 1bis:

$$N_{t+1} = N_t + rN_t \left(1 - \frac{N_t}{K}\right) - q \times E_t \times N_t \qquad (1\text{bis})$$

$$E_{t+1} = E_t + \alpha_t (P_t \times q \times E_t \times N_t - c \times E_t) \qquad (2)$$

where P_t is the price obtained per unit harvest, c the cost per unit effort, α_t a measure of how rapidly poachers respond to changes in profit, $(P_t \times q \times E_t \times N_t)$ is the total price for the quantity caught at time t, and $(c \times E_t)$ is the total cost associated with the hunting effort at time t (see Supplement for R script).

Price component

Theoretically, the price should be an increasing function of species rarity, i.e., inverse of population abundance (Eq. 3 from Courchamp et al. 2006):

$$P_t = p + v\left(\frac{K}{N_t}\right)^s \qquad (3)$$

where p is the price when the species was abundant, s and v are constants that determine how rapidly the price changes with respect to population size.

Cost components

Under the assumption of an AAE, exploitation cost per unit catch increases more slowly with rarity than the price, allowing exploitation to remain profitable (Courchamp et al. 2006). Illegal *shahtoosh* trading lasted for years (Huber 2005) and hunting of Tibetan antelope continued even at very low population sizes, suggesting that poaching effort remained profitable. Similarly to the price component, the cost per unit catch is a function of poached population size (Eq. 4, from Courchamp et al. 2006) since it will be more difficult to poach Tibetan antelope when they become rare (e.g., time consuming and expensive):

$$C_t = \frac{c}{q \times N_t} \qquad (4)$$

where c is cost per unit effort and C_t cost per unit catch.

Hunting response component

We included the number of additional poachers attracted by a higher profit with parameter α_t (Eq. 5, Courchamp et al. 2006):

$$\alpha_t = \frac{E_t}{\eta \times \text{time} \times (P_t \times N_t - C_t \times N_t)} \tag{5}$$

where η is a constant parameter representing the number of antelopes captured per week and time is the number of days per week.

A low value of α_t means that poachers responded slowly to changes in profit (i.e., similar to a constant hunting effort), whereas a high value reflects a rapid response by poachers to changes in profit.

We used 1-yr time steps for all equations. All the parameters of Tibetan antelope population dynamics and exploitation were either collected directly from the literature or calculated using the equations (Appendix: Table A3).

Incorporating conservation actions

We integrated three broad types of potential conservation actions into our model with and without an AAE (Eq. 1–1bis): a poaching cost increase, an antelope catchability reduction, and a poacher numbers reduction. First, the adoption of penalties for illegal trade (i.e., financial penalties and/or jail terms) equates to a poaching cost increase (Liang and Schwabach 2007). For example, in 2005, two poachers were sentenced to 13 years imprisonment and a penalty of about US\$625 for having killed 59 Tibetan antelopes (Xinhua News Agency 2005). For comparison, the average salary in 2005 was US\$127 per month in China (World Salaries 2007). This conservation measure specifically evaluates whether poachers are willing to risk high returns now and ignore penalties (i.e., heavily discounting the future). Secondly, the establishment of anti-poaching patrols or fully enclosed catchments could lead to the antelope catchability reduction. For example, IFAW/WTI (2001) initiated anti-poaching patrols consisting of 15 Forestry Police Stations and 5 anti-poaching forces, throughout the three nature reserves in the Tibetan antelope range. A third action might be attempted by encouraging the use of alternative wool resources by the local communities, like weaving pashmina, a fine cashmere wool from a special breed of sheep indigenous to high altitudes of the Himalayas (IFAW/WTI 2001). These three conservation actions were included in the models as follows.

Increase of poaching cost

We included a multiplicative term ω into the cost per unit effort parameter of the hunting effort Eq. 6 to represent the poaching cost increase:

$$\begin{cases} N_{t+1} = N_t + rN_t(1 - \frac{N_t}{K}) - q \times E_t \times N_t \\ E_{t+1} = E_t + \alpha_t(P_t \times q \times E_t \times N_t - (c \times \boldsymbol{\omega}) \times E_t) \end{cases} \tag{6}$$

where ω corresponds to an increase of exploitation cost, that is run from 2 to 10 times, by steps of 2. These values were chosen because financial penalties were 2 to 10 times higher than the cost of shawl production (Engler and Parry-Jones 2007).

Reduction of catchability level

We included a multiplicative term σ into the catchability parameter (Eq. 7):

$$\begin{cases} N_{t+1} = N_t + rN_t(1 - \frac{N_t}{K}) - (q \times \boldsymbol{\sigma}) \times E_t \times N_t \\ E_{t+1} = E_t + \alpha_t(P_t \times (q \times \boldsymbol{\sigma}) \times E_t \times N_t - c \times E_t) \end{cases} \tag{7}$$

where σ corresponds to a catchability reduction from 5% to 95%, by steps of 5%. A wide range of catchability reduction was chosen arbitrarily because there was no information about the reduction of the catchability rate that could be applied in this situation.

Decrease of the poacher numbers

We included a multiplicative term θ on the hunting effort Eq. 8 that corresponds to a reduction of poacher numbers, from 50% to 95%, with steps of 5%:

$$\begin{cases} N_{t+1} = N_t + rN_t(1 - \frac{N_t}{K}) - q \times E_t \times N_t \\ E_{t+1} = [E_t + \alpha_t(P_t \times q \times E_t \times N_t - c \times E_t)] \times \boldsymbol{\theta} \end{cases}. \tag{8}$$

Hence, a lower value of 50% was applied, thereby reducing the probability of overestimating poaching decrease, with maximum values of 90–95% representing the most likely reduction

(China Tibet Online 2006). A value of 100% was not used, because illegal import cases of *shahtoosh* shawl still occur (CITES 2012).

Finally, we applied a combined conservation action, which included all processes, in our model with and without an AAE. We assessed the potential success of these conservation measures by comparing the future population size and the net present value (Clark 1990). The expected NPV of applying the four conservation measures over different time horizons were calculated for two discount rates (i.e., 3 and 7%).

Data collection

Carrying capacity (K) and initial population size (N_o).—Intrinsic parameters of Tibetan antelope population dynamics were available in the literature (Appendix: Table A3). Their population size was at least one million at the beginning of the last century (Schaller 1998), which is the maximum population size of the species ever recorded (Sarkar et al. 2008). Hence, we fixed the carrying capacity (K) at one million individuals and also set the initial population size (N_o) at one million, as it was probably at carrying capacity before the decline started.

Growth rate (r).—Because we do not have precise estimates of the annual growth rate values, we used an interval, by steps of 0.01, between 0.01 and 0.08 (the highest limit found in the literature), instead of a fixed value.

Poaching (E).—We considered hunting effort as the number of poachers (Damania and Bulte 2007). Generally, a team of poachers consisted of ten or more people, with four teams per poaching session (IFAW/WTI 2001). Thus, we used a poaching effort per session of 40 poachers (Appendix: Table A3). Nevertheless, this hunting effort value might be underestimated because it is only based on organized bands, which do not include the majority of the poachers (Huber 2005). Indeed, much poaching was done by locals with foot traps and other simple equipment (Huber 2005). To account for this potential range of poachers, we included a wide range of hunting effort, between 40 and 80 by steps of 1.

Catchability (q).—The catchability of Tibetan antelope was calculated using $H = q \times E \times N$ (Milner-Gulland 2001). Fashion demand for *shahtoosh* shawls has led to the poaching of an estimated 20,000 individuals per year since 1980 (Sarkar et al. 2008). This set the Hunting rate (H) at 20,000. In 1980, the census population size (N) was determined as 250,000 individuals (East 1993, IUCN 2000), whereby the catchability of Tibetan antelope by poachers (q) would correspond to a value of 0.002 ($=H/(E \times N) = 20{,}000/(40 \times 250{,}000)$).

Cost (C_0 and c).—We obtained cost parameters from IFAW/WTI (2001). The cost estimates, including the price of hides and shawl production (obtaining raw wool, spinning, washing, wool dyeing), were approximately US\$213 (C_0). We used this to calibrate the profit level simulated in the model and to estimate the constant of cost per unit effort (c).

Price (P).—*Shahtoosh* shawls were sold at an estimated US\$250 ($=p$) (IFAW/WTI 2001). An estimate of the magnitude of the changes in the real profit of *shahtoosh* is given by IFAW/WTI (2001), and is considered a good indicator of general trends. Using Eq. 3 that establishes the relationship between the price and population abundance, we calculated v (=568) and s (=1.2) that define the speed at which the price changed with antelope population size.

Poacher response (α)

To estimate the value of the additional number of poachers who would be attracted by each additional dollar of profit, we considered that hunting technique did not change during the study period and we used a constant number of 385 antelopes captured per week (η).

We performed sensitivity analysis for all parameters using a classical "manual perturbation" of ±10% (Beissinger 1995; Appendix: Table A4).

Models without AAE

To test the assumption that Tibetan antelope populations suffered from an AAE during overexploitation, we compared the baseline model with and without AAE. We used Eqs. 1 and 1bis according to a population size threshold below which hunting ceases to be profitable, leading to its cessation. Because it was impossible to assess population size when poaching would stop, we tested seven thresholds: 1%, 5%, 10%, 20%, 30%, 40% and 50% of K. We chose to use a stop-hunting threshold compared with proportional harvesting, since it has been reported as

Table 1. Result of model fitting for (A) Tibetan antelope population size with a fixed growth rate and a variable hunting effort. Data from the period 1950–2003 was used to fit the models. (B) Optimal conservation action models, with a fixed growth rate and a variable hunting effort. Data from the period 1950–2011 was used to fit the models. The best model (boldface type) was chosen by using the AIC_c. The intercept (*k*), the slope (*l*), the degrees of freedom (df), log likelihood (logLike), ΔAIC_c and Akaike weight are shown. The hunting threshold is the percentage of the carrying capacity (*K*) below which hunting stops.

Model	Stop-hunting threshold	*k*	*l*	df	logLike	AIC_c	ΔAIC_c	Akaike weight
(A) Population exploitation models								
AAE model		**$2.24e^{+04}$**	**0.98**	**8**	**−110.64**	**231.27**	**0**	**0.36**
Non-AAE	1% K	$2.20e^{+04}$	0.98	8	−110.65	231.30	0.03	0.34
Non-AAE	5% K	$9.76e^{+03}$	0.99	8	−111.42	232.84	1.57	0.16
Non-AAE	10% K	$-2.31e^{+04}$	1.03	8	−112.35	234.70	3.43	0.07
Non-AAE	50% K	$-7.65e^{+05}$	1.76	8	−113.49	236.97	5.70	0.02
Non-AAE	20% K	$-1.29e^{+05}$	1.13	8	−113.51	237.03	5.76	0.02
Non-AAE	30% K	$-2.84e^{+05}$	1.28	8	−113.84	237.68	6.41	0.02
Non-AAE	40% K	$-4.89e^{+05}$	1.49	8	−133.84	237.69	6.42	0.01
(B) Conservation models with AAE model								
All actions combined		**$3.31e^{+04}$**	**0.97**	**13**	**−171.33**	**350.83**	**0**	**0.46**
Poacher reconversion		**$3.57e^{+04}$**	**0.97**	**13**	**−171.59**	**351.36**	**0.53**	**0.36**
Catchability decrease		$3.93e^{+04}$	0.96	13	−172.46	353.09	2.26	0.15
Cost per unit effort increase		$4.64e^{+04}$	0.95	13	−173.84	355.86	5.03	0.03

providing a more sustainable harvest (Lande et al. 1997, Sæther et al. 2010). The choice of a threshold harvest strategy implies here that no harvest occurs if the population falls below a certain threshold. Because the first two population size records had high values compared to the other population size records, we also ran the models with the 1980 and 1992 baselines (i.e., omitting these two high population sizes). This confirmed that these two values did not have any disproportionate influence on our results (Appendix: Table A5).

Model selection

We used an information-theoretic approach to compare models (Burnham and Anderson 2002). In an attempt to assess the presence or absence of an AAE, and determine which among the four conservation scenarios are more likely to be theoretically associated with the population recovery, we fitted the observed population size data (Table 1) using the *gls* function (*nlme library,* Pinheiro et al. 2014, with R version 2.14.2 software). We tested for the existence of temporal autocorrelation by comparing models with and without a correlation structure (corCAR1(), *nlme*). The AICc values (Akaike's Information Criterion corrected for small sample size) indicated that the model without correlation structure (AICc = 231.24, w = 0.73) fits to our data better than the model with a correlation structure (AICc = 236.57, w = 0.51). As a result, there was no evidence of temporal autocorrelation. Models were ranked according to their AIC_c and ΔAIC_c was computed for each model (AIC_c of the model minus the AIC_c of the "best model"). From the ΔAIC_c, we computed the Akaike weights of the models, which can be interpreted as the estimated relative strength of evidence that each model in the set is the "best model" (Burnham et al. 2011). We considered $\Delta AIC_c < 2$ as an acceptable threshold to select the model, following the suggestion of Arnold (2010). Model-selection approach was performed using the MuMIn package (Bartón 2012).

Results

Overexploitation with an AAE?

We found an exponential relationship with a negative slope between shawl price and population size (Fig. 1; Appendix: Table A6). This meant that when antelope population size became low, below the rarity threshold of 100,000 individuals, the price for shawls increased sharply. We also found evidence that a change in trend of population size occurred during the exploitation vs. conservation phases (Appendix: Table A9).

The AAE model outperformed the non-AAE models, but only when the non-AAE models had hunting thresholds above 10% of the initial

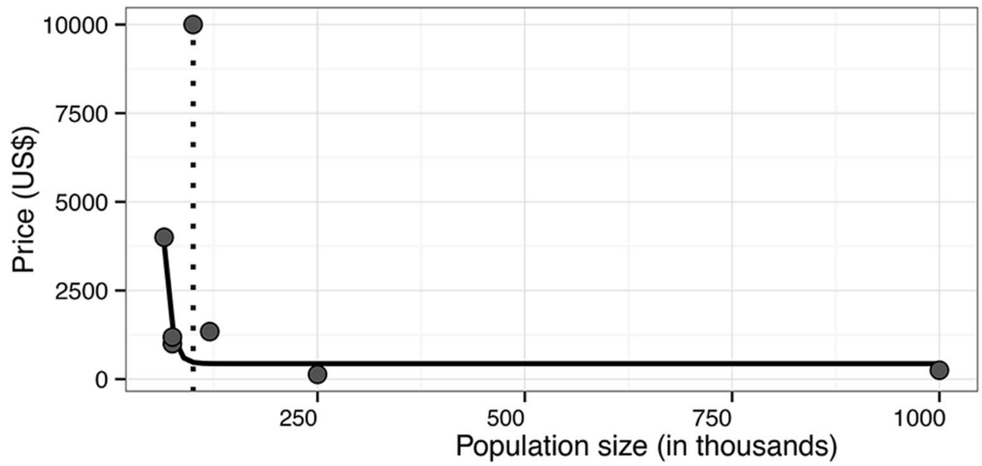

Fig. 1. Records of *Shahtoosh* price (US$, inflation corrected) versus Tibetan antelope population size (grey points) with predictions from the model fitted to the data (black line) (Appendix: Table A5). Dotted grey line: rarity threshold of species population size obtained by change-point analysis on a predicted curve ($Nr = 100{,}000$ individuals).

population size (Fig. 2, Table 1A; Appendix: Fig. A1). There were no substantial differences between the non-AAE models with 5% and 1% thresholds and the AAE model (Table 1A). Results were similar regardless of when the data was restricted (i.e., start date of 1980 or 1992; Appendix: Table A5 and Fig. A2).

The model including an AAE and a fixed growth rate value (i.e., 0.08) with a variable hunting effort (ranging from 40-80) fits the

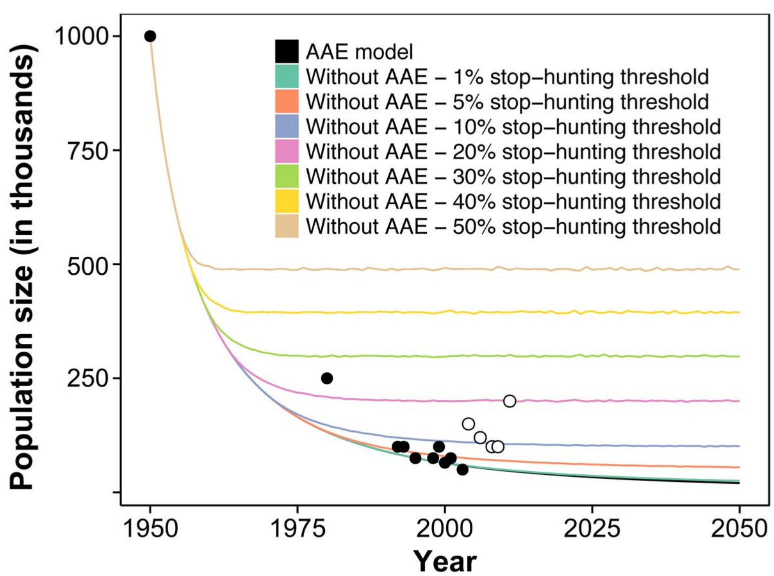

Fig. 2. Predicted Tibetan antelope population dynamics with and without an AAE between 1950 and 2050. Population dynamics were modeled with a fixed growth rate (0.08) and a variable hunting effort (40–80). Black line: AAE model; Other color lines: non-AAE models that assumed that antelope poaching is no longer profitable when the population is reduced to 1%, 5%, 10%, 20%, 30%, 40% or 50% of its carrying capacity. Closed points represent population size data before the establishment of conservation actions and open symbols represent population size data after the establishment of conservation actions.

population size data better than the model containing a variable growth rate between 0.01-0.08 and a constant hunting effort ($E = 40$), which predicted, on average, a slower decrease in population size (Appendix: Fig. A3a–b). Including a variable growth rate and a variable hunting effort simultaneously, showed a faster decrease of population size compared to models that maintained one of these two rates constant (Appendix: Fig. A4 and Table A7).

Tibetan antelope conservation

Role of conservation actions.—We evaluated the potential effects of conservation measures during the recovery phase with and without the presence of an AAE. The 'no intervention' scenario corresponds to the AAE-model (black line in Fig. 2). Overall, our results showed that increasing poaching cost per unit effort is likely to result in no effect on Tibetan antelope population dynamics i.e., similar to the 'no intervention' scenario (Fig. 3a; Appendix: Fig. A5a). Conversely, both the reduction of catchability and poacher numbers had potentially positive impacts on population dynamics (Fig. 3b–c; Appendix: Fig. A5b–c and Fig. A6a–b), although slightly less so for catchability reduction. Although the predicted increase was consistent with the population increase described by literature data after 2003, all conservation scenarios underestimated this increase. Our model, with a poacher numbers reduction (e.g., potentially switching to alternative livelihoods) (Fig. 3c) predicted a faster and less variable potential increase of population size than the model with catchability reduction (Fig. 3b; Appendix: Fig. A6). Overall, the model with a reduction of poachers, potentially due to a switch to alternative livelihoods, is the best explanatory model (Table 1B: df = 13, $\Delta AIC_c = 0.53$, Akaike weight = 0.36). This indicated that poacher numbers reduction is likely to be a very strong driver of Tibetan antelope population dynamics irrespective of the presence or absence of AAE. Furthermore, the simultaneous combination of conservation measures (Fig. 3d; Appendix: Fig. A5d and Fig. A6c) had the same predicted pattern as poacher numbers reduction alone (Fig. 3c; Appendix: Fig. A6b), although with a higher probability of being the best performing model (0.46 vs. 0.36). Regarding the NPV, there is not a large difference between the effects of a reduction of poacher numbers and all actions combined for either 3 or 7% discounting. Both alternatives showed a potential decrease in the benefits for poachers in the short-term, while increasing poaching cost and reducing catchability clearly favored an increase in the benefits for poachers (Appendix: Table A8 and Fig. A7). Hence, theoretically, reducing poacher numbers as the only measure may represent a rational policy in the short-term to sustain Tibetan antelope population size.

Long-term population size.—Because all conservation scenarios predicted different patterns of Tibetan antelope population dynamics in the short-term (until 2050), we also examined these scenarios in the longer-term. First, our results showed that not all of the conservation actions could potentially result in the recovery of the 1950 Tibetan antelope population size. The model with increased poaching costs (per unit effort) did not predict recovery, but a population crash instead (Fig. 3a). Increasing poaching cost had no effect on population recovery during the period 2003–2200, assuming a constant response of society and antelope population (Fig. 3a). The model with catchability reduction did not predict recovery of the population size but still predicted a potential increase of population size to 332,252 individuals by 2190, assuming an AAE, while the model without an AAE showed a theoretical population recovery in 2246 (Fig. 3b; Appendix: Fig. A6a). Regardless of the presence of an AAE, the model with all conservation scenarios combined did predict a potential full population size recovery faster than the model with poacher reconversion to pashmina (i.e., 2015 vs. 2019).

Discussion

The overexploitation of the Tibetan Antelope at low population sizes in conjunction with a rise in shawl price is a theoretical basis for the potential existence of an AAE. Our analysis supports the presence of an AAE, but only if poaching of Tibetan antelopes ceases before reaching 5% of its initial population size with the non-AAE models (i.e., the stop-hunting threshold). We found no evidence of an AAE if hunting continues when the population reaches 5% of the initial population size. In order to determine the definitive presence of an AAE, additional information is needed

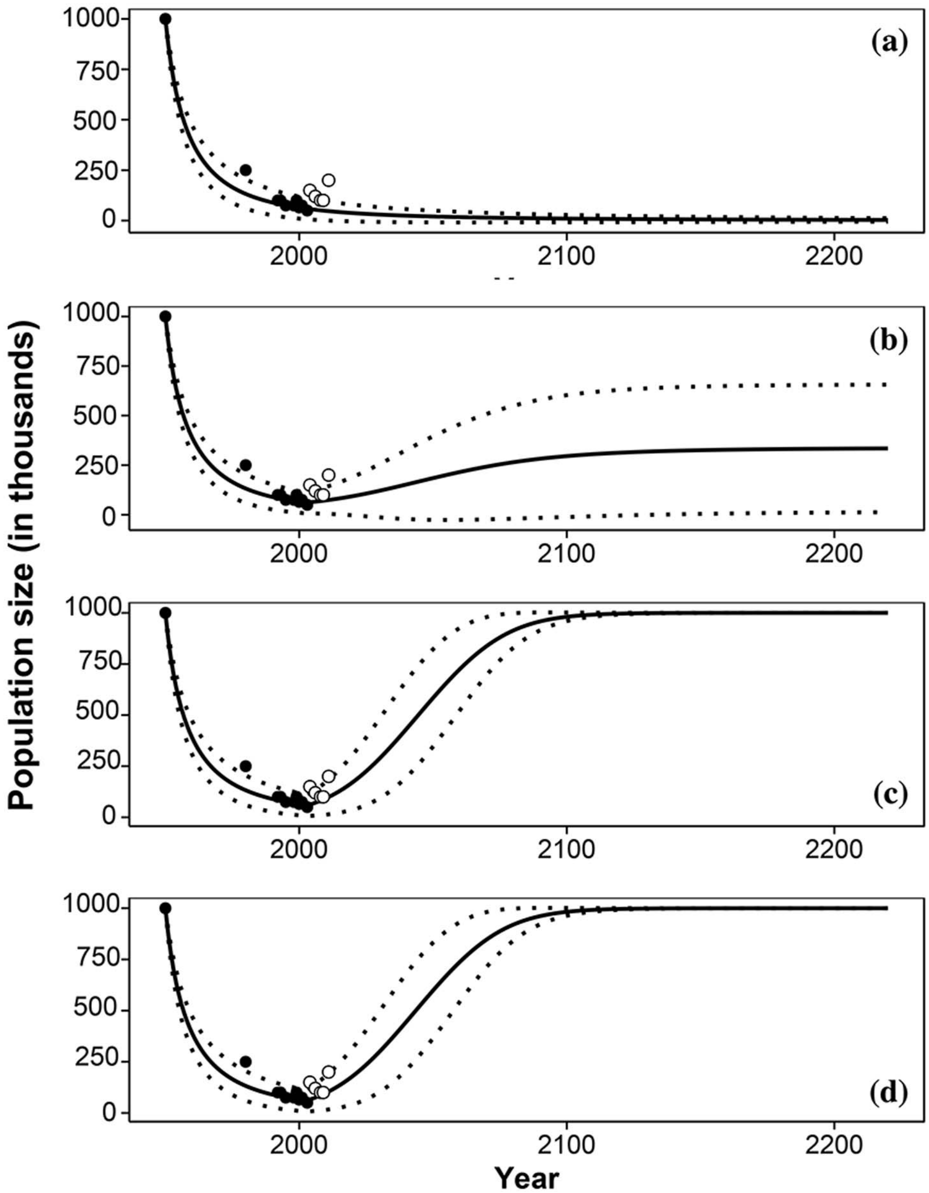

Fig. 3. Predicted Tibetan antelope population dynamics after incorporating conservation actions (from 2003) (a) poaching cost increase; (b) catchability reduction; (c) poacher numbers reduction; (d) all three actions combined. Black line: average predicted population size; Dotted line: standard deviation of the predicted population size; Population size data: black points before, and white ones after 2003. Population dynamics were modeled with a fixed growth rate (0.08) and a variable hunting effort (40–80).

regarding hunting dynamics at low population sizes for the Tibetan Antelope.

The growing concern for the protection of this species since 1996, limited the wool supply in the market. Simultaneously, studies observed a sudden increase of both price and poacher interest (Gopinath et al. 2003), consistent with the hypothesis of an AAE. Moreover, the growing controversy over the ban on the *shahtoosh* trade in Kashmir also caused public curiosity and increased the desire to possess it (Gupta 2011). Illegal *shahtoosh* trade was present from the 1970s to 2005 (IFAW/WTI 2001, Huber 2005) and has probably never completely ceased. Our results revealed that the Tibetan antelope population continued to be exploited even at a low population size, when it was most difficult to poach individuals. We found a low response to change in profit in the AAE model, which explained the similarity below 5% with a non-AAE model. However, the non-AAE model in the Tibetan antelope population revealed that poaching below 5% of the initial population size would still be profitable even if the poacher numbers were constant over time, although finding individuals would be extremely time-consuming. Moreover, we showed that wildlife trade bans were not sufficient to stop population decline, as illegal hunting was a very strong driver. However, it is likely that other factors may partially explain the species' decline, in particular competition with domestic livestock (Berger et al. 2013). Furthermore, these factors, and other threats that are likely to increase in the future, including climate changes or habitat losses, could limit its recovery (Sala et al. 2000).

In addition, the best model considered an average value for poaching effort of 60 poachers, suggesting that initially we had underestimated poaching effort (i.e., 40). Because of the lack of precise monitoring over the years, we only compared our results to the global trend of Tibetan antelope population size from 1950–2011. The necessary detailed demographic data are often not available, which makes it difficult to apply demographic models for many species and especially for rare species, as in the present study (Doak et al. 2005). In such situations, it is crucial to use a combination of different sources of demographic data to study population dynamics of rare species (Schaub et al. 2007). As a result, despite fragmentary demographic data, our theoretical model depicted remarkably well the decline of the population over five decades.

Importantly, our results also showed that even in presence of an AAE, adequate conservation actions could potentially rescue a species from an extinction vortex. Indeed, our results suggested that some conservation measures are likely to have significant effects on Tibetan antelope population dynamics. The strategy involving a reduction of the poaching level of 50–95%, predicted a potential positive impact on population dynamics and on poachers' benefits, with a global population increase by 90% (projection from 2003 to 2050), in accordance with trends observed recently. This means that alternative livelihoods, like pashmina, are likely to be the most important cause of Tibetan antelope population increase. Similarly Nielsen et al. (2014) have found that a salary for an alternative occupation had a significant strong negative effect compared to the magnitude of fines or patrolling frequency, on the probability of choosing to engage in hunting and trading bushmeat. Nevertheless, alternative livelihoods often have complex effects according to socioeconomic processes, and are not necessarily a substitute for direct poaching (Hill et al. 2012). At the local scale, poaching is indeed a major economic source and the availability of alternative economic opportunities can play a major role to stop poaching (Adhikari et al. 2005). On the contrary, the lack of effect of decreasing the profit on the recovery of the antelope population is due to the slow response to changes in profit. Consequently, even considering higher costs would not be sufficient to significantly reduce the hunting effort level in our results. This can be explained by the poachers' perception of economic incentives. It is likely that poachers were slow in adapting to changes in profit, as they probably still perceived it as profitable. In a similar study on the ivory trade, Burton (1999) predicted that a significant hunting effort would remain even if ivory prices were reduced substantially. Therefore, in our models, poachers are predicted to be willing to risk high returns now and ignore penalties, which concords with other studies regarding elephants (Clark 1973). Conversely, a study on the effects of governmental directives on Bisa wildlife use showed how hunter behavior in the Luangwa Valley, Zambia, changed as law enforcement increased (Freehling and Marks 1998). The model with reduced catchability predicted a potential increase of Tibetan antelope population size, until a total recovery for the non-AAE model. The combination of conservation actions was the best model statistically, but this model had a similar effect on population size than the most efficient action alone (i.e., reduction of poacher numbers), suggesting that using multiple actions in this particular case would be potentially less efficient (e.g., for economic reasons).

Therefore, our results suggested that the Tibetan antelope population could potentially increase, mainly through a reduction of poaching levels, for example by establishing alternative income sources for poachers. In addition, since we used a threshold harvest strategy in our models, if no control of illegal hunting is implemented, the population is likely to be rapidly driven into extinction, because poaching even a few individuals represents a large proportion of small populations (Sæther et al. 2010, Wittemyer et al. 2014).

Tibetan antelope populations are structured in age groups, by movement behavior (migratory or resident) and by individuals' use of space over time (calving areas or not) (Leslie and Schaller 2008), which was not considered in our models. Widespread anecdotal accounts and reports in the popular Chinese press suggested that poachers did not have any preferences for hunting sites (Bleisch et al. 2009) and males were poached as well as females (IFAW/WTI 2001, Liang and Schwabach 2007). Therefore, including population class structure was not necessary in order to model the Tibetan antelope population dynamics, although different sub-groups may differ in their vulnerability to poaching. Other natural and human factors not included in our models may also play a role in Tibetan antelope population dynamics, especially on their mortality, such as predators, diseases, parasites, starvation, inclement weather, and competition with livestock (Leslie and Schaller 2008). Notably, a recent study also suggested that increased grazing pressure by cashmere-producing goats may also lead to ecosystem degradation and competition with Tibetan antelope, which is likely to have a negative impact on their population (Berger et al. 2013). Therefore, reduction of the number of poachers in the future should also be accompanied by measures to preserve the Tibetan antelope's habitat in order to guarantee the maintenance of the positive effects of this conservation action on the its current population recovery. Nevertheless, the impact of these factors on its population dynamics is likely to be less important compared with poaching, which was described as the major threat during the 20th century (Ginsberg and Schaller 1999). In addition, the change of sensitivity parameters over time suggested that our results were less robust in the long-term. Finally, data in the literature suggest a population size of 200,000 individuals in 2011 while application of the best conservation action (i.e., reduction of poacher numbers) indicated a population size of about 100,000 individuals. None of the conservation scenarios considered in our model fully explained the Tibetan antelope population increase after 2003, which may suggest that important factors were omitted, or that the model calibration or quality of monitoring data were not optimal. However, despite being very simple compared to the complexity of actual population dynamics of large ungulates, our model was able to reproduce the observed trends remarkably well. Our model suggested that the Tibetan antelope was subject to high pressure from hunters which was driving it rapidly into an extinction vortex, and that voluntary conservation actions were so efficient that the species could escape this vortex, with definitive recovery if this trend could be maintained in the long term.

This case study is a potent illustration that a species plummeting towards extinction can be potentially saved, even when strong economic incentives are at stake. The Tibetan antelope is not the only species suffering from over-exploitation. For example, illegal exploitation of black rhinoceros and elephant populations have historically led to dramatic declines in these populations (Leader-Williams et al. 1990, Ferreira et al. 2012). Evaluation of adequate conservation measures have been intensively studied for some of these emblematic species (e.g., Black rhinos; Leader-Williams et al. 1990), while this remains poorly studied for other species. Meanwhile, the design and implementation of strong conservation actions is essential in order to preserve declining populations of endangered species. In this context, our study shows that conservation actions can be effective even when a population has lost 90% of its individuals in a few generations. This means that there may be effectively very few lost causes in conservation biology.

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Supplemental Material

Ecological Archives

The Appendix and the Supplement are available online: http://dx.doi.org/10.1890/ES15-00049.1.sm