Data-poor management of African lion hunting using a relative index of abundance

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Sustainable management of terrestrial hunting requires managers to set quotas restricting offtake. This often takes place in the absence of reliable information on the population size, and as a consequence, quotas are set in an arbitrary fashion, leading to population decline and revenue loss. In this investigation, we show how an indirect measure of abundance can be used to set quotas in a sustainable manner, even in the absence of information on population size. Focusing on lion hunting in Africa, we developed a simple algorithm to convert changes in the number of safari days required to kill a lion into a quota for the following year. This was tested against a simulation model of population dynamics, accounting for uncertainties in demography, observation, and implementation. Results showed it to reliably set sustainable quotas despite these uncertainties, providing a robust foundation for the conservation of hunted species.

management strategy evaluation | control rule | operating model | matrix model

Sustainable management of exploited biological resources is often hampered by insufficient information on either population size or the dynamic response to harvesting. In terrestrial trophy hunting systems, even though target species biology may be well studied, the population size itself is often poorly estimated. Abundance data are limited in time and space, making informed management decisions problematic. In response to economic pressure, quotas are often set too high, leading to population decline and a loss of long-term economic revenue (1). The trophy hunting of animals for sport can have significant conservation benefits (2–4), but there is an urgent need for methods that will allow sustainable management.

Deriving robust means to set sustainable limits to exploitation is now a well-developed science, increasingly applied to marine fisheries (5), and referred to as management strategy evaluation (MSE) (6). Within this framework, process-based simulations are used to test the performance of a quota setting algorithm (the control rule) against management targets. Including uncertainty in the projections allows development of a control rule that is robust to incomplete knowledge of resource status or its response to harvesting, implicitly conforming to the precautionary principle of resource management (7).

We derive a control rule that is able to set sustainable quotas in the absence of any information on population size and use MSE to evaluate its performance. The context is provided by lion (*Panthera leo*) hunting in sub-Saharan Africa, which exemplifies the problems associated with sustainable management of terrestrial hunting systems. Lion quotas are generally set by government and allocated to private hunt operators that then sell hunting safaris to individual clients. A successful hunt yields a fixed trophy fee, which is usually accrued by the local statutory authority. The daily fees (which are accrued regardless of the success of a hunt) conferred to hunt operators by paying clients can be an important source of revenue for local conservation and development (8). However, a formal mechanism for setting quotas is still missing and in the absence of reliable abundance data they are frequently set at unsustainable levels (9–11). The approach presented here therefore strengthens the theoretical foundation for sustainable trophy hunting practices for lions and data-poor hunting systems in general.

Steps toward more sustainable management of lion hunting have been made in Tanzania and Mozambique, where minimum age rules are applied (11). Males are sexually active around 4 y of age (12), and previous work has suggested that restricting hunting to males of age 6 y and older would allow a sustainable harvest regardless of the numbers killed (13, 14). However, there is still disagreement on whether it is practically feasible to age lions in the field (15). Some degree of noncompliance with age based criteria can therefore be expected. Furthermore, current unsustainable levels of offtake make hunters more likely to kill underage lions (because as populations decline individuals above the minimum age will become scarce).

To implement MSE, we first developed an age- and sex-structured, stochastic transition matrix operating model of lion dynamics that included the salient aspects of lion biology and reproduction, including density dependent fecundity and dispersal. Disruption to the social organization of a lion population through hunting of pride males leads to increased rates of infanticide (1, 13), potentially lowering its resilience. This important effect was also included, making cub survival directly related to the intensity of hunting. The model included a stochastic demographic process and random variation in the vital rates in response to assumed environmental fluctuations. To validate the model, it was shown to generate a population structure similar to empirical observations (Table S1). It was further tested under

Significance

Trophy hunting is a useful source of income for conservation. However, it remains contentious, not least because quotas for charismatic species in less-developed countries are often too high, contributing to population decline. The decline of lion populations across Africa continues and is not helped by the unsustainable management of hunting concessions. Best practice rests on the enforcement of a minimum age rule for hunting of males, which allows them to breed before they are killed. However, there is still no reliable method for setting quotas at a sustainable level. In this paper, we present such a method, which makes use of readily available data on the time needed to find and kill a lion, and demonstrate its efficacy through simulation.

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a range of constant harvest rates and demonstrated that lion populations are less able to sustain high quotas when females or younger males are hunted and that hunting older males increases the prospects for sustainability without jeopardizing trophy offtake (13, 14): when the minimum age of hunting is 2 y, the maximum sustainable harvest rate is only 0.10, but when male lions of 6 y of age and older are hunted the population is able to sustain a proportionate annual harvest rate of 0.95, with an approximate 50% increase in the annual number of lions killed.

The operating model was considered to be a reliable representation of lion dynamics and used to project the population forward in time, subject to a harvest specified by a control rule. The control rule is a simple algorithm that converts observational data into a quota (number of lions). In most lion trophy hunting systems, only indirect data on changes in population size are available, specifically the effort (safari days) required to kill a lion. Such data have found widespread application in resource management (16–18). Although efficacy of the hunt operator will likely influence the waiting time, they typically search with limited knowledge of lion whereabouts (not least because suitable lions of known location would have been killed during previous hunts) within a concession area of around 2,000 km^2 (8). Furthermore, safaris are usually combined with the hunting of other animals, making it more likely that the probability of a lion encounter will still be correlated with lion density. Nevertheless, when extracting an abundance signal from this type of data, it may be necessary to apply statistical modeling techniques of the type routinely used in fisheries (19, 20).

Empirical data provided for this study support our assumption that population density is the primary determinant of waiting time at the scale considered. Documented decline of local lion numbers over the period of data collection is associated with a 19% increase in mean waiting time (Fig. 1), as first noted by Packer et al. (10). There is also a close fit of the data to a negative binomial distribution (Fig. 1), parameterized by the mean μ and a dispersion parameter k, which is consistent with a standardized, random search process over space for aggregated individuals. Combined with knowledge of the logistics of hunting, we therefore assumed that changes in the average waiting time to find and kill a lion provide information on changes in abundance. The empirical data further provided an estimate of the uncertainty inherent in the observation process, allowing us to simulate observational data during MSE.

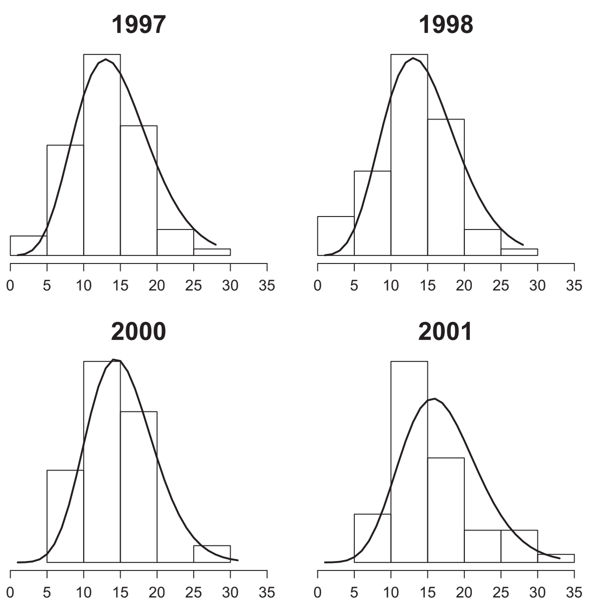

Fig. 1. Empirical probability distributions of the waiting time in days required to kill a lion. Empirical data are shown for years 1997, 1998, 2000, and 2001, with n = 76, 76, 55, and 53, respectively. The solid lines are the fitted negative binomial distributions with parameter values of μ = 13.5, 13.5, 14.3, and 16.0 and k = 13.6, 14.1, 30.5, and 21.3, respectively.

To derive a control rule that is able to make use of waiting time data, we begin with a sustainable harvest rate H, applied to the number of lions available to be hunted N [we stipulate that only males should be hunted with a minimum age of 6 y, consistent with recommendations made by Whitman et al. (13)]. The sustainable quota is therefore $Q = HN$. Using probabilistic arguments and assuming a random search of hunters across space, we obtain an inverse relationship between N and the mean waiting time to find and kill a lion $\mu = 1/cN$, where c is a constant (the catchability). Combining these two relationships, we can predict the sustainable quota using waiting time data only: $Q = H/c\mu$. To apply this control rule, we specify a target harvest rate of 0.8 for lions of age 6 and over and predict the expected waiting time (and therefore quota) 1 y into the future using regression methods. The catchability refers to the proportion of the total area covered by a single day of hunting. In the primary (base case) results presented here, it is assumed that the true value (referred to as c^*) is known by management and included in the control rule. Further simulations were carried out to test the potential consequences of an incorrect value (*SI Results*). In addition, we included a limit to the number of safari days equal to the maximum observed in the empirical data (33 d), so that if the hunt exceeded this duration, it was assumed to have failed. This bound placed a threshold on what is effectively the observed population size, below which hunting stops, in a manner analagous to that recommended by Lande et al. (21, 22). The catchability applied here resulted in a threshold of ~25 lions.

Finally, during hunting, lions were sampled at random and removed from the population according to the conditional probabilities of killing a lion that has been encountered. The aging of lions in the field is unfortunately not accurate (15), and it was therefore necessary to modify these probabilities to account for the fact that under age lions might be killed, deliberately or otherwise. Aging error has been described in previous work (13, 14), in relation to the minimum nose pigmentation used to identify a lion of suitable age to be hunted. For example, if a hunter kills a lion with ≥70% nose pigmentation, then there is a 95% chance that it is ≥6 y of age, but this drops to 62% when the nose pigmentation is ≥40%. Although this represents a single trait only, it was assumed to be representative of the hunter's efforts to age the lion. To fully incorporate noncompliance to the minimum age limit into the MSE, we performed stochastic projections for the full range of four minimum pigmentation values reported in Whitman et al. (14) (Table S2). Results were then integrated across these different compliance scenarios, with equal weighting for each.

Results

Having developed the necessary model components, performance of the control rule in maintaining a viable lion population under trophy hunting was evaluated through simulation. The MSE process was iterated forward in time, assuming a heavily depleted initial population, and including uncertainties in demography, observation, and compliance to the minimum age rule. At each iteration of the MSE, waiting time data were sampled from a negative binomial distribution, with a mean obtained from the density of male lions predicted by the operating model and a fixed dispersion. Performance was measured by tracking the realized harvest rate and number of males over a 30-y period. Because some noncompliance to the minimum age rule was incorporated in stochastic projections, performance was measured by recording the harvest rate and population size for the total adult male population (i.e., ≥4 y), for which the sustainable harvest rate is ~0.25. In addition we recorded the quota and success rate (proportion of quota filled) alongside other hunting and sustainability metrics (Table S3).

During the projection period the adult male population size increased at a rate of two per year from around 38 to 100 individuals while simultaneously increasing the quota from around 15 to 22 (Figs. 2 and 3). The hunting success rate increased from close to zero to 76%, with a simultaneous decrease in the waiting time from 30 to 23 d. Thus, despite stochasticity, the control rule is able to converge on a sustainable quota, which remains relatively stable throughout the projection period.

Our simulations confirmed that the hunting of younger lions has deleterious consequences for population size (Table S3), with maximum and minimum compliance scenarios yielding adult male population sizes of 100 and 95, respectively. The consequences are also apparent in the number of legal males killed, which is 8.6 and 6.3, respectively, with a quota of 16 lions for both scenarios. When compliance is low, a broader section of the population is exposed to hunting, short waiting times are maintained, and quotas are not reduced even though the overall population size is smaller. Although the control rule is able to converge on a level of exploitation that matches population productivity within the range of compliance scenarios considered, we note that more extreme noncompliance scenarios will have implications for sustainability of the population because the equilibrium population size will be smaller (i.e., use of the control rule does not negate the need for enforcment of age-based criteria).

Simulations were repeated over a range of catchability (c) values to test robustness of our results when catchability assumed by the control rule is different from the true value. An error of 90% in both directions led to a change in the median realized harvest rate of between 0.10 and 0.14, well below the estimated sustainable harvest rate of 0.25 (Fig. S1). Hence, qualitative performance of the control rule was robust to error in the assumed catchability.

Discussion

Traditional methods of setting a hunting quota rely on abundance information so that a specified proportion of the target population can be removed each year. Unfortunately, this information is often of poor quality or completely absent, particularly in developing countries. We have described a means by which hunting quotas can be set with no information on population size. This method was tested through simulation of a lion hunting system in its entirety, including observation, management, implementation of quota, and the population dynamic response. Despite uncertainty in all these components, we showed that the control rule can ensure sustainable hunting practices. The control rule therefore contributes to the theoretical basis for management of trophy hunting systems, where only a single individual is hunted at a time (although selectivity is not a prerequisite), and to lion hunting in particular.

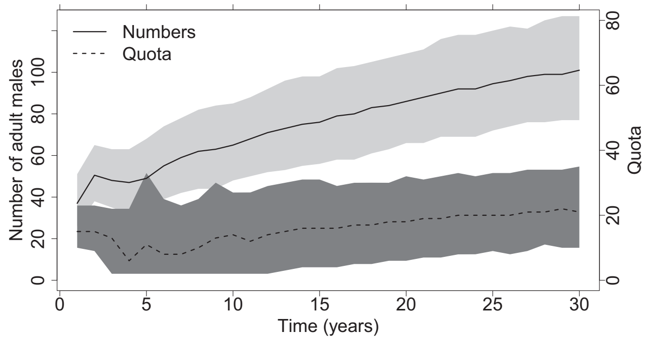

Fig. 2. Dynamic system response over time. Median changes in the number of adult males (≥4 y of age) and the quota are shown following initialization of the system. Shaded regions represent 95% CIs across stochastic iterations, taking into account uncertainty in the dynamics, observation, and compliance to the minimum age criterion.

The practical application of this work requires understanding of the assumptions on which it is based, and we will deal with these in turn. The first assumption is that changes in the waiting time to find and kill a huntable individual provide information on changes in the population size. Waiting time is likely to be influenced by a range of factors, including location, experience of the hunt operator, simultaneous hunting of other game, and the use of baits, of which annual changes in density is only one. Were the data available, it would be possible to standardize the waiting times by accounting for these factors statistically (19, 20). If this were not possible, it would be safer to consistently aggregate data from defined safari operations to prevent annual changes in the contributing hunt operators affecting the mean waiting time. There is also inherent noise that arises from the stochastic nature of observation, which will be larger when the number of observations is small. Mean waiting times generated during the simulated observation process had a maximum coefficient of variation of around 20%, decreasing to 10% when 10–15 lions were killed annually. This degree of variation appears to be small enough for the control rule to perform well. Noting that the simulated observation uncertainty was deliberately greater than that estimated from the empirical data, and assuming our observation model to be accurate, we nevertheless recommend that the average waiting time should be estimated from at least 20 kills for the control rule to be applied in a practical setting.

The second assumption that needs to be considered is compliance of the hunters. The waiting time will only change in response to changes in the population size if hunters are prepared to wait longer and potentially forfeit the trophy if a lion above the minimum age cannot be found. If instead hunters shoot younger lions, then the waiting time will be unchanged and the quota will not be adjusted. Although the control rule is robust to some degree of noncompliance, sustainability will still be threatened because the equilibrium population size will be smaller. The dynamics at low population sizes are not well represented by the operating model applied here, and we therefore cannot evaluate precisely what degree of noncompliance could be tolerated. We can nevertheless conclude that use of the control rule does not circumvent the need for enforcement of minimum age restrictions on hunting. However, the setting of a sustainable quota will give a declining population an opportunity to recover. Given that hunters have a preference for older lions, this itself will encourage compliance as the population grows.

The generality of the control rule, and an understanding of assumptions inherent to its application, should allow practical use of the methods presented in this paper across a variety of data-poor systems. A paucity of accurate information on population size is common to most exploited biological resources, requiring management methods that can be applied despite this lack of knowledge. The MSE framework provides the means to test such methods (6, 23) and is beginning to be used for terrestrial systems (17, 18, 24, 25). The scientific formality that underpins MSE provides the credibility and transparency needed to enforce quota restrictions. Because the testing procedure can be tuned to accommodate the concerns of any stakeholder, MSE has been shown to facilitate consensus among resource users and the support of management action (26) and is thus an effective tool for conservation.

Materials and Methods

Operating Model. Lion population dynamics were described by the nonlinear matrix model

$$\mathbf{N}_{t+1} = \mathbf{M}_t(\mathbf{N}_t - \mathbf{k}_t), \qquad [1]$$

with the transition matrix $\mathbf{M}_t$ a function of density and time-dependent vital rates and $\mathbf{k}_t$ a vector of numbers killed. Ten different cohorts of 1 y each

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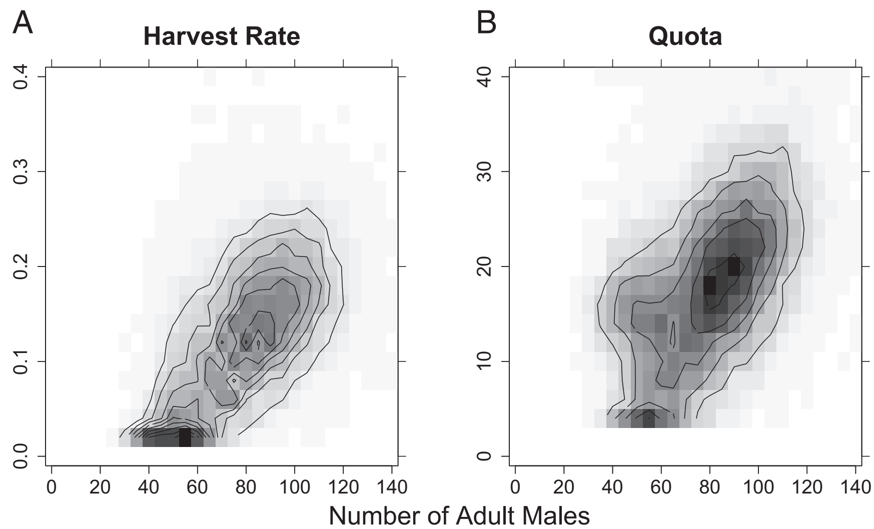

Fig. 3. Contour plots illustrating stochastic convergence of the control rule. Contours enclose the state space occupied by the system over time and iterations, integrated over compliance scenarios. (*A*) Realized harvest rate of adult males. (*B*) Quota set by the control rule. As the system evolves over time there is a progression toward higher numbers, an increased harvest rate, and higher quotas. Because noncompliance to the minimum age rule is allowed, we report the realized harvest rate for all adult males (≥4 y of age). The system converges on an adult male harvest rate of ∼0.16, associated with a population size of 99 adult males and an annual quota of 22 lions, with a 76% hunting success rate.

were represented and are listed in Table S4. The population was split into cub, subadult, and adult cohorts by sex. Both males and females were considered mature at 4 y of age (12, 27), with the maximum ages represented being ≥4 and ≥6 y for females and males, respectively.

The matrix $\mathbf{M}_t$ was subdivided into components $\mathbf{B}_n$, $\mathbf{A}$, and $\mathbf{S}_t$, representing birth, aging, and survival, respectively. Infanticide was incorporated by making cub survival an increasing function of realized adult male survival (following hunting). A further matrix $\mathbf{Q}_n$ contained the density-dependent probabilities of dispersal for both males and females, which imposed a constraint on population growth. We could therefore write $\mathbf{M}_t = \mathbf{B}_n\mathbf{Q}_n\mathbf{A}\mathbf{S}_t$. These components are described in detail in the *SI Materials and Methods* along with explorations of the simulated dynamics.

Observational Data. Fig. 1 shows distributions of the waiting times (d) from Zimbabwe for years 1997, 1998, 2000, and 2001. Also shown are the best fit negative binomial distributions, parameterized by the mean μ and dispersion k, illustrating that waiting times are well described by this distribution. The negative binomial was a better fit than the Poisson distribution [using methods described by Bliss and Fisher (28) and Lindsey (29)], consistent with an aggregated (nonuniform) distribution of individuals across space. We can also observe that waiting times do not appear to be bounded by a maximum number of days (i.e., there are no peaks at the upper extremes of the distributions).

The simulation of observational data for MSE requires us to specify a relationship between the lion population size and the waiting time for a kill d, including the associated negative binomial uncertainty. If N_j is the number of males of age j, then a complete description of the observation process would specify both k and a relationship between the vector of N_j values and the mean number of days μ. To describe the relationship between male numbers and μ, we note that the level of aggregation has no effect on the mean. With this in mind, we consider a mean age-specific density of lions over space D_j and an effective area A covered by a single day of hunting. This area encompasses the area within which lions are potential targets and may include both the area covered during the hunt and the area from which lions are attracted to any baits laid. A successful hunt is broken down into the probability of encountering a lion P^e, and the conditional probability of killing a lion once it has been encountered P^k (Table S2). The probability of encountering a lion of age j on any given day is $P_j^e = D_jA$, and the probability of a successful hunt is $P^s = \sum D_jAP_j^k$. We are then able to derive the expected waiting time required to kill a single lion

$$\mu = \frac{1}{P^s}. \quad [2]$$

To ensure that $P^s \le 1$, $A \le 1/\sum D_jP_j^k$ (i.e., the hunting area does not exceed the area in which we would expect to kill one lion). Thus, A is limited by the density of lions. Intuitively, this assumption simply states that a hunter will not continue searching over space after a lion has been encountered and killed.

From Eq. **2**, and assuming $D_j = N_j/A^t$, where A^t is the total area considered, we obtain a relationship between the expected waiting time to kill a single lion and the population size

$$\mu = \frac{1}{c\sum N_jP_j^k}, \quad [3]$$

where $c = A/A^t$ is a constant referred to as the catchability and equal to the proportion of the total area covered in a single day of hunting. This definition has a direct analog in the fisheries literature (30). We note that Eq. **3** is related to an unbiased estimate of population abundance: $\hat{N} = n/\alpha p$, where n is the number of individuals observed in the study area, α is the proportion of the population area covered, and p is the conditional probability of observing an individual that is present (21, 31), setting $n = 1$, $\alpha = \mu c$, and $p = P_j^k$ constant across ages.

When multiple lions are hunted during one season

$$\mu_i = \frac{1}{c\sum P_j^k\left[N_j - K(i,j) + 1\right]}, \quad [4]$$

for each of i successful hunts. The function $K(i,j)$ is equal to the cumulative number of lions of age j that have been killed, up to and including hunt i. Following a single successful hunt, $K = 1$, giving Eq. **3**. The numbers N_j were provided by the operating model. Thus, the waiting time for hunt i in year t is described by the negative binomial distribution

$$d_{ti} \sim NB(\mu_{ti}, k), \quad [5]$$

which was used to simulate observational data on waiting times given the constants c and k (*SI Materials and Methods*).

Control Rule. Derivation of the control rule proceeds as follows. We begin with a sustainable harvest rate H, applied to the total number of males above the minimum age N. The sustainable quota is therefore $Q = HN$. From Eq. **3**, assuming that $P_j^k = 1$ for all lions above the minimum age and 0 otherwise, this gives $\mu = 1/cN$ and

$$Q = \frac{H}{c\mu}, \quad [6]$$

describing a relationship between the sustainable quota and the waiting time. Introducing a time dimension, to obtain a quota for the next year Q_{t+1}, we must predict a value for μ_{t+1}. To achieve this, we take a forward difference of the derivative $\frac{d\mu}{dt}$ and substitute in for μ_{t+1} to get

$$Q_{t+1} = \frac{H}{c}\left[\frac{d\mu}{dt}\Delta t + \mu_t\right]^{-1}. \quad [7]$$

The derivative $\frac{d\mu}{dt}$ was approximated using a regression over the previous 5 y $\{\hat{\mu}_{t-4}, \ldots, \hat{\mu}_t\}$. To provide input for the control rule, we obtain our observed waiting time for each year $\hat{\mu}_t$ from the arithmetic mean

$$\hat{\mu}_t = E[d_t] = \frac{1}{K_t}\sum_{i=1}^{K_t} d_{ti}, \quad [8]$$

given K_t kills and with d_{ti} obtained from Eq. **5**. The quota was thus set according to the control rule

$$Q_{t+1} = \hat{H}_t\left[c(\hat{m} + \hat{\mu}_t)\right]^{-1}, \quad [9]$$

where $\hat{m}$ is the gradient of $\hat{\mu}$ over the previous 5 y, and $\hat{H}$ is a realized value corresponding to the target rate multiplied by the success rate (proportion of quota filled). To ensure a reasonable range of quota values, we imposed bounds of $2 \le Q_{t+1} \le \hat{H}_t/c$. Finally we rounded output from the control rule to the nearest integer.

The control rule therefore requires us to assume (*i*) a minimum age at which male lions are hunted; (*ii*) a sustainable harvest rate specified as a proportion of the targeted males above the minimum age H; and (*iii*) a catchability c that indicates the proportion of the total area covered by a day of hunting. According to the recommendations from previously published work (13), we fixed the minimum age at 6 y. Preliminary explorations with the operating model showed it to reaffirm suggestions that high harvest rates can be sustained if lions ≥5 y are hunted. We chose a target value of $H = 0.8$, which corresponded to a conservative estimate of the maximum sustainable rate. We assume c is not known by management and treat it as a sensitivity (i.e., we tested how sensitive the results were to an inaccurate value for c in the control rule; *SI Results*).

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