
#### Abstract

Establishing historical baselines of species' populations is important for contextualising present-day population trends, identifying significant anthropogenic threats, and preventing a cultural phenomenon known as 'shifting baseline syndrome'. However, our knowledge of historical baselines is limited by a lack of direct observation data on species abundance pre-1970. We present historical data of species-specific fur harvests from the Canadian government and Hudson's Bay Company as a proxy for estimating species abundance over multiple centuries. Using stochastic stock reduction analysis originally developed for marine species, we model historical population trends for eight mammals, and assess population trends based on two different baseline years: 1850 and 1970. Results show that population declines are significantly greater when using an 1850 baseline, as opposed to a 1970 baseline, and for four species, the population trend shifted from a population increase to a decrease. Overall, the median population change of the eight species changed from a $15 \%$ decline for 1850 , to a $4 \%$ increase for 1970 . This study shows the utility of harvest data for deriving population baselines for hunted terrestrial mammals which can be used in addition to other historical data such as local ecological knowledge. Results highlight the need for developing historically relevant population baselines in order to track abundances over time in threatened species and common species alike, to better inform species conservation programs, wildlife management plans and biodiversity indicators.


Keywords: Historical baselines; shifting baseline syndrome; population estimation; mammal conservation; Hudson's Bay Company; North America

## 1. Introduction

Species population declines and extinctions undermine the functioning and resilience of ecosystems on which humans and wildlife depend (Cardinale et al. 2012; Oliver et al. 2015). To monitor and respond to species losses, changes in population abundance are used as a sensitive metric of change (Collen et al. 2011; Shoemaker and Akçakaya 2015) and have been incorporated into globally adopted biodiversity indicators such as the Living Planet Index, which tracks changes in vertebrate population abundance from 1970 (Collen et al. 2009). However, data on population abundance typically become scarcer beyond a few decades from the present, prior to the implementation of species monitoring programmes (Willis et al. 2005; Bonebrake et al. 2010).

Knowledge of historical populations acts as an antidote to 'shifting baseline syndrome'; a phenomenon in which with each new human generation comes a lowered expectation of a species population norm (Pauly 1995; Kahn and Friedman 1995; Soga and Gaston 2018). Historical population baselines have many practical policy implications, for example when defining population recovery and conservation legacy, deciding harvest quotas, and influencing the general public's perception of a species (Papworth et al. 2009; Davies, Colombo, and Hanley 2014; Roman et al. 2015; Akcakaya et al. 2018; see Figure 1a). Additionally, estimating historical populations can help to differentiate between a population trend that is unidirectional or cyclical, such as the Atlantic Multidecadal Oscillation inducing bidirectional changes in fish abundance (Jackson et al. 2001; Willis et al. 2007; Sundby and Nakken 2005; see Figure 1b). Without long-term measurements, observers may misattribute downward phases of natural population cycles as human-caused population declines (Koslow and Couture 2013). Finally, historical population data can help to identify historic drivers of population change (see Figure 1c), which is important for quantifying the relative significance of each past and present threat in order to develop threat-specific management strategies and inform future scenario modelling (Baker and Clapham 2004; Pinnegar and Engelhard 2008).

Many techniques available to reconstruct historical population baselines emerged from the discipline of marine historical ecology (Lotze and Worm 2009). Faced with the need to sustainably manage fish stocks, fisheries researchers have used recorded history (e.g. 'local ecological knowledge') (Sáenz-Arroyo et al. 2005; Turvey et al. 2010), archaeogenomic data (e.g. analysis of relative stable isotope concentrations) (Finney et al. 2002), and fish stock assessments from historical catch data (Myers and Worm 2003; Baker and Clapham 2004) to extrapolate population size over time and capture stock collapses that pre-date direct monitoring.

Recorded history has also provided us with historical population estimates for terrestrial species, although not as frequently as in the marine realm. These studies are extremely valuable in painting a picture of past population condition (Cole and Woinarski 2000; Rowe and Terry 2014), but with each historical data source comes its own unique set of limitations. For instance, museum and fossil records are often
patchy and taxonomically biased, and local ecological knowledge generally only covers a couple of generations spanning less than 100 years (Miller 2011). Here, we add to our growing knowledge on reconstructing population baselines by focussing on harvest data of terrestrial mammals as another data source which holds great potential in historical baseline reconstruction.

Reports from the Hudson's Bay Company (HBC), Canada, have been previously used to document lynx and muskrat population cycles (Elton and Nicholson 1942a; Elton and Nicholson 1942b), predator-prey dynamics of lynx and snowshoe hare (Krebs et al. 1995), and the potential roles of climate, productivity and disease in these cycles (Gamarra and Solé 2000; Yan et al. 2013; Row et al. 2014). Here, we (a) show the utility of these harvest data to reconstruct historic populations by applying a stochastic population model first developed for marine vertebrates (Christensen 2006), (b) use these population reconstructions to demonstrate that baselines differ when using over 100 years of data compared to less than 50 years of data and (c) show that choice of different baseline years results in different interpretation of estimated population trends.

## 2. Methods

### 2.1 Reconstructing historical abundance trends

To reconstruct historical trends in terrestrial mammal abundance, we used a stochastic stock reduction analysis (SSRA) originally developed by Walters et al. (2006) to analyse trends in fish populations. This method uses a simple growth model, and can be applied to species for which we have limited knowledge of life history parameters and catch-per-unit-effort (Kimura, Balsiger, and Ito 1984). The model and method outlined below was described in detail by Christensen (2006) for establishing historical baselines of marine mammals:

$$
\begin{equation*}
N_{t+1}=N_{t}+r_{\max } N_{t}\left(1-\frac{N_{t}}{K}\right) e^{w_{t}}-C_{t} \tag{1}
\end{equation*}
$$

where $N_{t}$ is the number of individuals in a population at time $t, r_{\text {max }}$ is the intrinsic rate of increase, $K$ is the carrying capacity, $\mathrm{w}_{t}$ is the error term at time $t$, and $C_{t}$ is the number of individuals harvested annually. The population is assumed to be at $K$ at the start of hunting, and the model implies that there are no errors in our records of $C_{t}$.

Using a Bayesian approach, we randomly drew from a uniform prior distribution of $K$, which was bounded by a lower and an upper estimate, and normal prior distributions of $r_{\underline{m a x}}$ and $\mathrm{w}_{t}$ values. We used process error terms ( $\tau_{\underline{w}}$ ) for the standard deviation of
 calculated the likelihood $(L)$ of deriving the known abundance estimate for the current population $\left(y_{t}\right)$ based on the estimated $N_{t}$ using eq. 2 :

$$
\begin{equation*}
L\left(y_{t} \mid r_{\max } K, w_{t}\right)=n\left[\log \left(\sigma_{y}\right)+\frac{1}{2} \log (2 \pi)\right]+\sum_{i}=\frac{z_{t}^{2}}{2 \sigma_{y}^{2}} \tag{2}
\end{equation*}
$$

where $n$ is the number of ewrrent pepulation-abundance estimates $\left(y_{t}\right)$ available for each species, $\sigma_{\mathrm{y}}$ is the observation error (standard deviation of the abundance estimate, $\nu_{t}$, and $z_{t}$ is the log-normal residual, calculated as:

$$
\begin{equation*}
z_{t}=\log \left(N_{t}\right)-\log \left(y_{t}\right) \tag{3}
\end{equation*}
$$

Equation 1 to 3 were repeated 200,000 times. Generated $N_{t}$ values were then resampled using the importance sampling procedure by Schnute (1994) and McAllister and Ianelli (1997), to estimate a posterior probability density function. Finally, we calculated the median and the $95 \%$ credible interval of the $N_{t}$ trajectory, after computing the marginal posterior distributions of $K$.

### 2.2 Harvest data

We conducted a literature search for fur trade records of Canadian mammals from the Hudson's Bay Company (HBC). The HBC fur clothing business, originally Londonbased, became established in Canada in 1670 in response to the UK demand for fur and the abundance of furbearing mammal species in Canada (Simmons 2007). Expanding its area of influence over time, the company monopolised the North American fur trade from 1821 onward, and eventually operated over an area that spanned around one quarter of the extent of North America (Erickson 2015; Colpitts 2017; Company 2017).

Published annual HBC sales accounts for 25 mammals were acquired from Poland (1892) for the time period 1751 - 1847 and Jones (1914) for the time period 1848 1909. Additional HBC data was supplied for the American badger (Taxidea taxus), beaver (Castor canadensis) and Canadian lynx (Lynx canadensis) by the NERC Centre for Population Biology (NERC Centre for Population Biology 2010), Hewitt (1921) and Elton and Nicholson (1942) respectively. Canadian fur data for 1919 1970 were retrieved from Novak (1987) and data for 1970 - 2009 from the National Bureau of Statistics (NBS), Canada (2010). Using the individual number of furs across datasets as a proxy for the number of individuals taken for trade resulted in time series harvest data for 25 mammal species ranging from 1722 - 2009 (electronic supplementary material, Table S 1 ). Of these 25 species, only thirteen had harvest data from two or more continuous datasets up to and including 2009 (the last year of data available from NBS, Canada). Harvest data for species modelled is supplied in the supplementary material (Table S2).

Jones' (1914) data represented the number of furs sent to HBC headquarters, and Poland (1892) represented the year the fur was sold at the London auctions; therefore, these data were backdated by two years and one year respectively following Elton and Nicholson (1942a). All time-series had a data gap for the years 1910 - 1918 and 2002. We estimated values for these years using a log-linear interpolation for all species except the lynx. Due to the 9 -year cyclic nature of the lynx harvest data, a linear interpolation was applied around the peak year (1914) of the cycle for 1910-1914, and $1914-1918$.

We can be fairly confident that the numbers reported from annual sales accounts is an underestimate of the actual number of individuals caught (e.g., Elton and Nicholson 1942a), due to escape from traps, illegal trade by trappers, lost or stolen carcasses in transit to London's auction house, bookkeeping errors, etc. Although statistical approaches such as employing a correction factor are available to counteract the undocumented loss, we select to estimate the minimum population decline based on reported numbers only.

### 2.3 Informative priors

In order to perform the Bayesian SSRA model, population growth rate $\left(r_{\max }\right)$ and recent population current abundance estimate(s) $\left(y_{t} ; 1979-2008\right)$ in eq. 1 and 2 were gathered from peer-reviewed publications for each species (electronic supplementary material, Table S3; Table S4). If countrywide population abundance estimates ( $y_{t}$ ) for Canada were unavailable, province-wide abundance estimates were extrapolated to the entire current species range within Canada. Species range maps were downloaded from the IUCN Red List of Threatened Species (IUCN 2014). Of the 13 species with harvest data, muskrat (Ondatra zibethicus), marten (Martes americana), red fox (Vulpes vulpes), mink (Neovison vison), and coyote (Canis latrans) had no countrywide or province-wide estimates of $\mathfrak{y}_{f}$ abundance and were therefore removed from the study.

The contribution of observation error $\left(\sigma_{y}\right)$ to the total error term $(\underline{\kappa} \equiv \underline{0.1}$ ) for each species was determined by selection criteria adapted from Christensen (2006), based on the source and uncertainty $(p)$ associated with the abundance estimate, $\underline{y}_{t}$.
Province-wide extrapolations of $y_{t}$ were assigned the highest uncertainty and direct estimates were assigned the lowest uncertainty (electronic supplementary material, Table S5). The remaining proportion of the total error term was allocated to the independent process error $\left(\tau_{w}\right)$, which represented the ecologically mediated fluctuations within a true population size (Ahrestani, Hebblewhite, and Post 2013), such that $\underline{\sigma}_{y} \equiv \sqrt{\underline{p}} \underbrace{*} \sqrt{\underline{\kappa}}$ and $\underline{\tau}_{\underline{w}} \equiv \sqrt{\underline{1-p}} \underline{*}^{\underline{\underline{\kappa}}}$.

As no data exist on historical carrying capacity $(K)$ of populations, we estimated priors for $K$ from historical range maps from the 1900s for each species obtained from Seton (1909). We georeferenced each species' map in ArcGIS v9.3 (ESRI 2008) to obtain the historical range in $\mathrm{km}^{2}$, assuming all of the historical range was viable
habitat. We collected present day minimum and maximum density estimates (individuals $/ \mathrm{km}^{2}$ ) from the literature and produced a lower and upper bound for $K$ by extrapolating the density estimates to the historical range. A uniform prior distribution was then drawn, which assumes that $K$ is constant over time (electronic supplementary material, Table S6). We carried out elasticity analyses to assess the impact of variation in our estimates of informative priors on population change.

### 2.4 Analysis of historical baselines

We reconstructed historical population trajectories for eight species; the American badger, Arctic fox (Vulpes lagopus), beaver, black bear (Ursus americanus), bobcat (Lynx rufus), Canadian lynx, fisher (Martes pennanti) and polar bear (Ursus maritimus). We quantified population change for each species as follows:

$$
\begin{equation*}
\text { Population Change }=\frac{N_{2009}-N_{b}}{N_{b}} * 100 \tag{4}
\end{equation*}
$$

where $N_{b}$ represents the population estimated at the given baseline year $b$. Population change was estimated for two baseline years: 1) 1850, the earliest year that all species had available data; and 2) 1970, the baseline year of the Living Planet Index (McRae, Deinet, and Freeman 2017). We then conducted a $t$-test to assess the difference in population change across the two baselines. We also calculated the median population change for all eight species under the two baselines and recorded the degree and direction of change.
2.5 Single versus multiple threats causes of mortality

Modelling population estimates based on fur trade alone overlooks other reasons animals are removed by humans; fur trade, trophy hunting, self-defense, illegal kills, individuals found dead, and handling by scientists. We applied the SSRA to another dataset for the polar bear, substituting fur trade records from 1970 onwards with data published by the IUCN Species Survival Commission (SSC) Polar Bear Specialist Group, that documents number of bears killed between 1970-2008 from all causes listed above (Derocher and Commission. 1998; Lunn et al. 2002; electronic supplementary material, Table S7).

### 2.6 Elasticity analysis

We carried out elasticity analysis (de Kroon et al. 1986) to examine the relative effect of parameter selection on model prediction. We independently halved and doubled each model parameter in turn (intrinsic growth rate ( $r_{\max }$ ), number of individuals harvested $\left(C_{t}\right)$, current pepulation size abundance estimate $\left(y_{t}\right)$, historical carrying capacity $(K)$, and observation error $\left(\sigma_{y}\right)$ ), and calculated elasticities $(e)$ of the 1850 2009 population change, where higher $e$ means higher proportional change in the parameter-population (de Kroon et al. 1986; Benton and Grant 1999; Hunter, Moller,
and Fletcher 2000). Y represents the population change caused by the altered parameter, $X$ :

$$
\begin{equation*}
e=\frac{\% \Delta Y}{\% \Delta X} \tag{5}
\end{equation*}
$$

All analyses were carried out in the statistical software RStudio version 1.0.143 (RStudio Team 2015).

## 3. Results

### 3.1 Analysis of historical baselines

The median population change across the eight species for 1850 - 2009 was a $15 \%$ decrease ( $-0.1 \% / \mathrm{yr}$ ), whereas populations between $1970-2009$ showed a $4 \%$ increase $(0.1 \% / \mathrm{yr})$ (paired t -test: $\mathrm{t}=-3.036,1$ d.f. $=7, p=0.002, n=8$; Table 1, Figure 3a).
Choice of baseline year resulted in a switch from a downward population trend for the period 1850 - 2009 to an upward trend for 1970 - 2009 for four species (Arctic fox, bobcat, polar bear, beaver) (Figure 3b; Table S8; Figure S1). Six species exhibited a more severe annual rate of population change for the $1850-2009$ period-as oppesed to the compared to trends derived from a 1970 baseline (Table 1; Figure 3b), with this pattern holding for five species when the annual rate of population change is considered (Table 1).

### 3.2 Single versus multiple threats-causes of mortality

Analysis of the polar bear data that encompassed all recorded mortality events from 1970 onwards shows that an additional 294 (range $=-57$ to 538 ) individuals were killed in comparison to the number harvested for furs alone (electronic supplementary material, Table S7). This altered the polar bear population decline using the 1850 baseline from $22 \%$ based on fur harvest data alone to $41 \%$ using the IUCN/SSC data (Figure 4).

### 3.3 Elasticity analysis

Parameters ranked in order of lowest to highest elasticity (proportional change in the population) were observation error, carrying capacity, harvest data, current population abundance estimate and intrinsic growth rate (Figure 5, Electronic supplementary material, Table S9). In other words, small changes to intrinsic growth rate and abundance estimates cause larger alterations to the model output. Species ranked in order of lowest to highest average elasticity for all informative priors were fisher, black bear, American badger, arctic fox, bobcat, polar bear, Canadian Lynx and beaver.

## 4. Discussion

Our study demonstrates that for eight species of Canadian mammals, choice of baseline year greatly affects our understanding of historic population change. Collectively, using an 1850 baseline year rather than 1970 significantly altered the population trend. Analysis of individual species demonstrated that deriving population change from the 1850 baseline resulted in four species shifting from a population increase since 1970 to a population decrease of between 0 and $-22 \%$ since 1850, and the magnitude of annual population change becoming more severe for six species (Figure 3). Interestingly, the polar bear, the only species to be listed as Vulnerable on the IUCN Red List (Wiig et al. 2015), was one of the four species to show a shift in population trend. From 1850, the population declined, reflecting the polar bear's IUCN conservation status, whereas the trend from 1970 showed the population as increasing.

Population time-series data allow for the detection of declines before species reach critical status (Balmford and Bond 2005; Di Fonzo et al. 2016; Collen et al. 2011). However, few long-term population studies used data more than 100 years old (e.g., $15 \%$; Bonebrake et al. 2010). Biodiversity indicators that are reliant on such population time series data, such as the Living Planet Index (LPI), therefore often operate on baselines set to post-1950 (Bonebrake et al. 2010). At least for temperate systems, the LPI dataset may not date back far enough to detect often precipitous population declines which occurred prior to 1970 (Watson et al. 2005). For example, while some population recovery is observed in Europe since 1970 (Deinet et al. 2013), species are often recovering from declines which had reduced populations to a fraction of their historical population sizes by or prior to 1970. These short-term baselines are likely a result of the relatively recent advent of conservation biology in the 1970s and 1980s and corresponding emergence of long-term monitoring data for ecology and conservation (Collen et al. 2009).

In this study, we were able to model seven species currently listed as Least Concern on the IUCN Red List and not assessed under the Canadian Wildlife Species at Risk assessment (COSEWIC 2019). However, for five relatively common species: muskrat, marten, red fox, mink, and coyote that we collected harvest data for, a lack of recent population estimates at the regional or national scale prevented population modelling. Species are rarely subject to monitoring until declines are apparent and they may be of conservation concern (Bonebrake et al. 2010), while threatened species are often prioritised for monitoring, given limited financial resources and capacity (Gaston and Fuller 2008). As we are frequently witnessing population declines in common species, it is imperative that population monitoring also targets abundant or common species (Collen et al. 2011). This proactive approach enables early detection of declines, rather than a late reactive response when a species has already declined extensively, thus approaching extinction. This is of particular importance as abundant species play important parts in the functioning and maintenance of ecosystems (Winfree et al. 2015).

The strengths of using HBC data to estimate population change is the consistent unit over time (number of furs traded) and high temporal resolution (annual data), which overcome limitations oftentimes associated with historical records (Balmford and Bond 2005; Mcclenachan, Ferretti, and Baum 2012). While HBC data provides a very unique set of data, hunting statistics are available in many countries (e.g. Agetsuma 2018), and have a long tradition in regions such as Europe (Deinet et al. 2013; Hewitt and Hewitt 2015). Hunting bag records were used in a recent study to analyse longterm population trends across a number of European countries for several game bird, ungulate and carnivore species, although the study only reached back as far as 1970 (Reimoser and Reimoser 2017). In the UK, the voluntary National Gamebag Census was formally established in 1961 but resulting records on game birds and predatory species extend back to 1900 for many species (Whitlock, Aebischer, and Reynolds 2003; Aebischer and Baines 2008). Models such as the one utilised in this study play an important role not just in deriving generalised trends, but also population estimates using such data repositories. Hunting statistics can then complement, or be used in tandem with, data from different sources such as transgenerational local ecological knowledge to obtain historical population baselines.

Despite our robust methods, population estimates from historical information such as harvest data are of lower quality than those derived from direct counts and current population monitoring, and uncertainty surrounding the estimates is inevitably greater. While some losses are not reported, resulting in a potential underestimate of the population (see methods 2.2), the spatial pattern of hunting that occurred throughout Canada in the past is likely to lead to an overestimate of hunting offtake of species. Hunting efforts saw a large westward expansion between 1783-1821, driven in large part by local depletion of beaver in the 'Canadian Shield' (Hope 2016; Figure 2). New areas such as the Red River Settlement, which was established in 1811, would have allowed access to previously unharvested subpopulations of mammals, and a boost to total harvest numbers. On the other hand, sources suggest that HBC was attempting to conserve beaver and bison in the 1820s (Colpitts 2017), presumably by enacting policies to help local population recovery, thus lowering total harvest. These local variations in harvest effort are not visible in our dataset, and the impact of uncertainty on our population estimates is illustrated by the mid-range elasticity of our model to a halving and doubling of harvest data (c) (Figure 5; Table S7). To some degree, our baseline of 1850 may help circumvent some of the previous geographical shifts or expansions in hunting effort. However, next steps should endeavour to account for spatial variation in hunting records over time by adding a spatially explicit component to the stock reduction analysis.

In addition to hunting, other drivers of population change are likely to impact our species, and focus on only a single cause of population offtake is likely to underestimate population trends over time. Substituting IUCN/SSC data on polar bear mortality via direct contact with humans into the final 40 years of our model changed the estimated decline from $25 \%$ (based on fur hunting data alone) to $41 \%$ (Figure 4).
As well as providing hunting numbers, the IUCN/SSC polar bear data also includes 'individuals found dead'. This statistic includes mortality events which may be human-mediated or a result of natural causes, such as starvation from lack of sea ice. While hunting is a key human-mediated impact, it is but one of several sources of population decline facing mammals in North America (Brook, Sodhi, and Bradshaw 2008; Grooten and Almond 2018; Spooner, Pearson, and Freeman 2018).
Other anthropogenic drivers of population change such as habitat loss and the introduction of non-native species are not included in this analysis, again rendering our estimates conservative. For example, habitat loss affected the vast majority of threatened mammals in Canada, with direct human-caused mortality coming second (Imre and Derbowka 2009). Although modelling the impacts of all negative and positive anthropogenic effects on abundance is beyond the scope of this study, we can be fairly certain that these threats would play a role in determining the population size, intrinsic growth rates and carrying capacity within regions of Canada. As anthropogenic threats are dynamic (Wilcove et al. 1998), the degree of impact on the population will also alter over time. This highlights the need to quantify the impact of other threats which may influence these population parameters differentially over time (e.g. land use change altering carrying capacity) and incorporate these into baseline population models. One way of achieving this could be to allow carrying capacity K to vary across the time frame of our model in response to observed range contractions. In choosing a baseline for constructing historic population trends, we are ourselves guilty of ignoring what happened to our species prior to our chosen year of 1850. However, we recognize that the fur trade existed far back beyond this. Hunting for fur was carried out by Native Americans and European settlers alike; during the $17^{\text {th }}$ century, the French owned the monopoly of the Canadian fur trade and by 1717, HBC had set up six trading posts (Voorhis 1930). By 1850, the fur trade had impacted wildlife on the east coast; between 1860 and 1920 the sea mink (Neovison macrodon) reportedly went extinct (Mowat 2012; Black, Reading, and Savage 1998). While we use 1850 to demonstrate the importance of a historical baseline for as many species as possible, the term 'baseline' is not used here to imply a 'start' date, nor do we claim that one date will suffice. Rather, historical baselines should be viewed as a sliding window, and in conservation, it is important to move that window as far back as possible through history, to provide better context for species' current population status.

## 5. Conclusions

By failing to estimate historical baselines, we may miss the historical demise of populations which have been exploited by humans since at least the $18^{\text {th }}$ century in Europe and North America (Deinet et al. 2013), and adversely influence our perception of what constitutes species population norms. This may affect how scientists, decision makers and the general public perceive the growth of a population as a result of conservation action and species protection. While in many northern hemisphere regions, population recovery to an 1850 (or earlier) baseline may no
longer be viable, due to the extensive anthropogenic land use change that has occurred in the interim, our current understanding of population recovery may focus on population sizes which are too small and could leave populations vulnerable to future threats or dependent on continued conservation action. We encourage the use of well-documented and quantifiable historical records in developing population baselines, thus establishing a broad temporal scale over which to analyse species population trends. Armed with such data, we can improve our communication about population declines and set ambitious goals for realistically achievable population recovery (Akcakaya et al. 2018), make better-informed conservation management decisions, and improve our historical ecological awareness.

## Supporting Materials

All datasets supporting this article have been uploaded as part of the supplementary material.

## Declaration of competing Interests

We have no competing interests to declare.

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## Tables and Figures

Table 1. Estimated percentage population change from 1850 and 1970 to 2009 for the eight modelled species. Mean population values are presented in bold and confidence intervals are presented in brackets.

| Species | 1850 <br> population | $1970$ <br> population | $2009$ <br> population | $\begin{aligned} & 1850-2009 \\ & \text { total }(\& \\ & \text { annual) } \\ & \text { population } \\ & \text { loss or gain } \\ & (\%) \end{aligned}$ | 1970-2009 <br>  <br> annual) <br> population <br> loss or gain $(\%)$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Arctic fox | 133,000 | 132,000 | 133,000 | 0 (0) | 1 (0.02) |
| Canadian lynx | 262,000 | 258,000 | 290,000 | 11 (0.06) | 12 (0.32) |
| Beaver | 4,730,000 | 3,730,000 | 4,440,000 | -6 (-0.04) | 19 (0.49) |
| Bobcat | 50,300 | 44,100 | 47,000 | -7 (-0.04) | 7 (0.17) |
| Polar bear | 20,300 | 13,900 | 15,800 | -22 (-0.14) | 14 (0.35) |
| Black bear | 831,000 | 414,000 | 390,000 | -53 (-0.33) | -6 (-0.15) |
| Fisher | 167,000 | 157,000 | 7,000 | -96 (-0.60) | -96 (-2.45) |
| American badger | 518,000 | 175,000 | 83,800 | -84 (-0.53) | -52 (-1.34) |



Figure 1. Schematic of hypothetical population trends highlighting the benefits of establishing a historical baseline through (A) providing better context on the extent of decline, thus allowing for better population recovery scenarios when advising on recovery targets (blue arrows signify extent of known decline), (B) identifying a trend through different time series lengths (represented by blue arrows) and discriminating between true decreasing trends and misattributed trends caused by population cycles, and (C) estimating the impact on populations from known drivers of decline captured through use of historical baselines.


Figure 2. The approximate locations of all Hudson's Bay Company trading posts that were operating in 1927 in North America, adapted from Elton and Nicholson (1942a).


Figure 3. Percentage change in population estimates using two different baseline years: 1850-2009 and 1970-2009 for (A) species cumulatively (t-test: $p<0.05 ; 1970$ : $4 \%, 1850:-14.5 \%$ medians $\pm$ S.E, $n=8$ ), and $(B)$ species-specific population estimates.


Figure 4. Population trajectories for polar bear, using, from 1970, (A) Canadian government annual fur harvest data and (B) IUCN/SSC statistics on number of polar bears annually killed in Canada. Pink bars are the annual fur harvest (right-hand axis), the blue solid line and blue dashed lines are the population projection and the $95 \%$ median confidence intervals respectively; the current Canada-wide population estimate is shown by the red dots (left-hand axis).


Figure 5. Elasticity analysis for each species, showing how population change between 1850-2009 altered when each parameter was doubled ( +50 ) and halved ( -50 ) for number of individuals caught ( $C_{t}$, orange lines); carrying capacity $(K)$ lower bound and carrying capacity upper bound (blue lines); original SSRA estimate (black line); intrinsic growth rate ( $r_{\max }$, green lines); standard deviation altered to 0.9 (grey line); eurrent pepulation abundance estimate(s) ( $y_{i}$; purple lines); observation error ( $\sigma$ y, pink lines).

# Choice of baseline affects historical population trends in hunted mammals of North America 

In memory of Dr. Ben Collen

Amy C. Collins ${ }^{1 *}$, Monika Böhm ${ }^{2}$, Ben Collen ${ }^{3}$
${ }^{1}$ Wildlife, Fish and Conservation Biology, University of California, Davis, Shields Avenue, CA, 95616, USA
${ }^{2}$ Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK
${ }^{3}$ Centre for Biodiversity \& Environment Research, Department of Genetics, Evolution \& Environment, University College London, London WC1E 6BT, UK
*Corresponding author (phone number: +1 530760 9139; email: accollins@ucdavis.edu)


#### Abstract

Establishing historical baselines of species' populations is important for contextualising present-day population trends, identifying significant anthropogenic threats, and preventing a cultural phenomenon known as 'shifting baseline syndrome'. However, our knowledge of historical baselines is limited by a lack of direct observation data on species abundance pre-1970. We present historical data of species-specific fur harvests from the Canadian government and Hudson's Bay Company as a proxy for estimating species abundance over multiple centuries. Using stochastic stock reduction analysis originally developed for marine species, we model historical population trends for eight mammals, and assess population trends based on two different baseline years: 1850 and 1970. Results show that population declines are significantly greater when using an 1850 baseline, as opposed to a 1970 baseline, and for four species, the population trend shifted from a population increase to a decrease. Overall, the median population change of the eight species changed from a $15 \%$ decline for 1850 , to a $4 \%$ increase for 1970 . This study shows the utility of harvest data for deriving population baselines for hunted terrestrial mammals which can be used in addition to other historical data such as local ecological knowledge. Results highlight the need for developing historically relevant population baselines in order to track abundances over time in threatened species and common species alike, to better inform species conservation programs, wildlife management plans and biodiversity indicators.


Keywords: Historical baselines; shifting baseline syndrome; population estimation; mammal conservation; Hudson's Bay Company; North America

## 1. Introduction

Species population declines and extinctions undermine the functioning and resilience of ecosystems on which humans and wildlife depend (Cardinale et al. 2012; Oliver et al. 2015). To monitor and respond to species losses, changes in population abundance are used as a sensitive metric of change (Collen et al. 2011; Shoemaker and Akçakaya 2015) and have been incorporated into globally adopted biodiversity indicators such as the Living Planet Index, which tracks changes in vertebrate population abundance from 1970 (Collen et al. 2009). However, data on population abundance typically become scarcer beyond a few decades from the present, prior to the implementation of species monitoring programmes (Willis et al. 2005; Bonebrake et al. 2010).

Knowledge of historical populations acts as an antidote to 'shifting baseline syndrome'; a phenomenon in which with each new human generation comes a lowered expectation of a species population norm (Pauly 1995; Kahn and Friedman 1995; Soga and Gaston 2018). Historical population baselines have many practical policy implications, for example when defining population recovery and conservation legacy, deciding harvest quotas, and influencing the general public's perception of a species (Papworth et al. 2009; Davies, Colombo, and Hanley 2014; Roman et al. 2015; Akcakaya et al. 2018; see Figure 1a). Additionally, estimating historical populations can help to differentiate between a population trend that is unidirectional or cyclical, such as the Atlantic Multidecadal Oscillation inducing bidirectional changes in fish abundance (Jackson et al. 2001; Willis et al. 2007; Sundby and Nakken 2005; see Figure 1b). Without long-term measurements, observers may misattribute downward phases of natural population cycles as human-caused population declines (Koslow and Couture 2013). Finally, historical population data can help to identify historic drivers of population change (see Figure 1c), which is important for quantifying the relative significance of each past and present threat in order to develop threat-specific management strategies and inform future scenario modelling (Baker and Clapham 2004; Pinnegar and Engelhard 2008).

Many techniques available to reconstruct historical population baselines emerged from the discipline of marine historical ecology (Lotze and Worm 2009). Faced with the need to sustainably manage fish stocks, fisheries researchers have used recorded history (e.g. 'local ecological knowledge') (Sáenz-Arroyo et al. 2005; Turvey et al. 2010), archaeogenomic data (e.g. analysis of relative stable isotope concentrations) (Finney et al. 2002), and fish stock assessments from historical catch data (Myers and Worm 2003; Baker and Clapham 2004) to extrapolate population size over time and capture stock collapses that pre-date direct monitoring.

Recorded history has also provided us with historical population estimates for terrestrial species, although not as frequently as in the marine realm. These studies are extremely valuable in painting a picture of past population condition (Cole and Woinarski 2000; Rowe and Terry 2014), but with each historical data source comes its own unique set of limitations. For instance, museum and fossil records are often
patchy and taxonomically biased, and local ecological knowledge generally only covers a couple of generations spanning less than 100 years (Miller 2011). Here, we add to our growing knowledge on reconstructing population baselines by focussing on harvest data of terrestrial mammals as another data source which holds great potential in historical baseline reconstruction.

Reports from the Hudson's Bay Company (HBC), Canada, have been previously used to document lynx and muskrat population cycles (Elton and Nicholson 1942a; Elton and Nicholson 1942b), predator-prey dynamics of lynx and snowshoe hare (Krebs et al. 1995), and the potential roles of climate, productivity and disease in these cycles (Gamarra and Solé 2000; Yan et al. 2013; Row et al. 2014). Here, we (a) show the utility of these harvest data to reconstruct historic populations by applying a stochastic population model first developed for marine vertebrates (Christensen 2006), (b) use these population reconstructions to demonstrate that baselines differ when using over 100 years of data compared to less than 50 years of data and (c) show that choice of different baseline years results in different interpretation of estimated population trends.

## 2. Methods

### 2.1 Reconstructing historical abundance trends

To reconstruct historical trends in terrestrial mammal abundance, we used a stochastic stock reduction analysis (SSRA) originally developed by Walters et al. (2006) to analyse trends in fish populations. This method uses a simple growth model, and can be applied to species for which we have limited knowledge of life history parameters and catch-per-unit-effort (Kimura, Balsiger, and Ito 1984). The model and method outlined below was described in detail by Christensen (2006) for establishing historical baselines of marine mammals:

$$
\begin{equation*}
N_{t+1}=N_{t}+r_{\max } N_{t}\left(1-\frac{N_{t}}{K}\right) e^{w_{t}}-C_{t} \tag{1}
\end{equation*}
$$

where $N_{t}$ is the number of individuals in a population at time $t, r_{\max }$ is the intrinsic rate of increase, $K$ is the carrying capacity, $\mathrm{w}_{t}$ is the error term at time $t$, and $C_{t}$ is the number of individuals harvested annually. The population is assumed to be at $K$ at the start of hunting, and the model implies that there are no errors in our records of $C_{t}$.

Using a Bayesian approach, we randomly drew from a uniform prior distribution of $K$, which was bounded by a lower and an upper estimate, and normal prior distributions of $r_{\text {max }}$ and $\mathrm{w}_{t}$ values. We used process error terms $\left(\tau_{w}\right)$ for the standard deviation of $\mathrm{w}_{t}$ values. This generated a $N_{t}$ trajectory which was dependent on $C_{t}$ (eq 1). We then calculated the likelihood $(L)$ of deriving the known abundance estimate for the current population $\left(y_{t}\right)$ based on the estimated $N_{t}$ using eq. 2 :

$$
\begin{equation*}
L\left(y_{t} \mid r_{\max } K, w_{t}\right)=n\left[\log \left(\sigma_{y}\right)+\frac{1}{2} \log (2 \pi)\right]+\sum_{i}{ }_{=}^{n} \frac{z_{t}^{2}}{2 \sigma_{y}^{2}} \tag{2}
\end{equation*}
$$

where $n$ is the number of abundance estimates $\left(y_{t}\right)$ available for each species, $\sigma_{y}$ is the observation error (standard deviation of the abundance estimate, $y_{t}$ ), and $z_{t}$ is the lognormal residual, calculated as:

$$
\begin{equation*}
z_{t}=\log \left(N_{t}\right)-\log \left(y_{t}\right) \tag{3}
\end{equation*}
$$

Equation 1 to 3 were repeated 200,000 times. Generated $N_{t}$ values were then resampled using the importance sampling procedure by Schnute (1994) and McAllister and Ianelli (1997), to estimate a posterior probability density function. Finally, we calculated the median and the $95 \%$ credible interval of the $N_{t}$ trajectory, after computing the marginal posterior distributions of $K$.

### 2.2 Harvest data

We conducted a literature search for fur trade records of Canadian mammals from the Hudson's Bay Company (HBC). The HBC fur clothing business, originally Londonbased, became established in Canada in 1670 in response to the UK demand for fur and the abundance of furbearing mammal species in Canada (Simmons 2007). Expanding its area of influence over time, the company monopolised the North American fur trade from 1821 onward, and eventually operated over an area that spanned around one quarter of the extent of North America (Erickson 2015; Colpitts 2017; Company 2017).

Published annual HBC sales accounts for 25 mammals were acquired from Poland (1892) for the time period 1751 - 1847 and Jones (1914) for the time period 1848 1909. Additional HBC data was supplied for the American badger (Taxidea taxus), beaver (Castor canadensis) and Canadian lynx (Lynx canadensis) by the NERC Centre for Population Biology (NERC Centre for Population Biology 2010), Hewitt (1921) and Elton and Nicholson (1942) respectively. Canadian fur data for 1919 1970 were retrieved from Novak (1987) and data for $1970-2009$ from the National Bureau of Statistics (NBS), Canada (2010). Using the individual number of furs across datasets as a proxy for the number of individuals taken for trade resulted in time series harvest data for 25 mammal species ranging from 1722-2009 (electronic supplementary material, Table S1). Of these 25 species, only thirteen had harvest data from two or more continuous datasets up to and including 2009 (the last year of data available from NBS, Canada). Harvest data for species modelled is supplied in the supplementary material (Table S2).

Jones' (1914) data represented the number of furs sent to HBC headquarters, and Poland (1892) represented the year the fur was sold at the London auctions; therefore, these data were backdated by two years and one year respectively following Elton and Nicholson (1942a). All time-series had a data gap for the years 1910 - 1918 and 2002. We estimated values for these years using a log-linear interpolation for all species except the lynx. Due to the 9-year cyclic nature of the lynx harvest data, a linear interpolation was applied around the peak year (1914) of the cycle for 1910-1914, and $1914-1918$.

We can be fairly confident that the numbers reported from annual sales accounts is an underestimate of the actual number of individuals caught (e.g., Elton and Nicholson 1942a), due to escape from traps, illegal trade by trappers, lost or stolen carcasses in transit to London's auction house, bookkeeping errors, etc. Although statistical approaches such as employing a correction factor are available to counteract the undocumented loss, we select to estimate the minimum population decline based on reported numbers only.

### 2.3 Informative priors

In order to perform the Bayesian SSRA model, population growth rate $\left(r_{\max }\right)$ and current abundance estimate(s) $\left(y_{t} ; 1979-2008\right)$ in eq. 1 and 2 were gathered from peer-reviewed publications for each species (electronic supplementary material, Table S 3 ; Table S 4 ). If countrywide abundance estimates $\left(y_{t}\right)$ for Canada were unavailable, province-wide abundance estimates were extrapolated to the entire current species range within Canada. Species range maps were downloaded from the IUCN Red List of Threatened Species (IUCN 2014). Of the 13 species with harvest data, muskrat (Ondatra zibethicus), marten (Martes americana), red fox (Vulpes vulpes), mink (Neovison vison), and coyote (Canis latrans) had no countrywide or province-wide estimates of abundance and were therefore removed from the study.

The contribution of observation error $\left(\sigma_{y}\right)$ to the total error term $(\kappa=0.1)$ for each species was determined by selection criteria adapted from Christensen (2006), based on the source and uncertainty $(p)$ associated with the abundance estimate, $y_{t}$. Province-wide extrapolations of $y_{t}$ were assigned the highest uncertainty and direct estimates were assigned the lowest uncertainty (electronic supplementary material, Table S5). The remaining proportion of the total error term was allocated to the independent process error $\left(\tau_{w}\right)$, which represented the ecologically mediated fluctuations within a true population size (Ahrestani, Hebblewhite, and Post 2013), such that $\sigma_{y}=\sqrt{p} * \sqrt{\kappa}$ and $\tau_{w}=\sqrt{1-p} * \sqrt{\kappa}$.

As no data exist on historical carrying capacity $(K)$ of populations, we estimated priors for $K$ from historical range maps from the 1900s for each species obtained from Seton (1909). We georeferenced each species' map in ArcGIS v9.3 (ESRI 2008) to obtain the historical range in $\mathrm{km}^{2}$, assuming all of the historical range was viable habitat. We collected present day minimum and maximum density estimates
(individuals $/ \mathrm{km}^{2}$ ) from the literature and produced a lower and upper bound for $K$ by extrapolating the density estimates to the historical range. A uniform prior distribution was then drawn, which assumes that $K$ is constant over time (electronic supplementary material, Table S6). We carried out elasticity analyses to assess the impact of variation in our estimates of informative priors on population change.

### 2.4 Analysis of historical baselines

We reconstructed historical population trajectories for eight species; the American badger, Arctic fox (Vulpes lagopus), beaver, black bear (Ursus americanus), bobcat (Lynx rufus), Canadian lynx, fisher (Martes pennanti) and polar bear (Ursus maritimus). We quantified population change for each species as follows:

$$
\begin{equation*}
\text { Population Change }=\frac{N_{2009}-N_{b}}{N_{b}} * 100 \tag{4}
\end{equation*}
$$

where $N_{b}$ represents the population estimated at the given baseline year $b$. Population change was estimated for two baseline years: 1) 1850, the earliest year that all species had available data; and 2) 1970, the baseline year of the Living Planet Index (McRae, Deinet, and Freeman 2017). We then conducted a $t$-test to assess the difference in population change across the two baselines. We also calculated the median population change for all eight species under the two baselines and recorded the degree and direction of change.

### 2.5 Single versus multiple causes of mortality

Modelling population estimates based on fur trade alone overlooks other reasons animals are removed by humans; fur trade, trophy hunting, self-defence, illegal kills, individuals found dead, and handling by scientists. We applied the SSRA to another dataset for the polar bear, substituting fur trade records from 1970 onwards with data published by the IUCN Species Survival Commission (SSC) Polar Bear Specialist Group, that documents number of bears killed between 1970-2008 from all causes listed above (Derocher and Commission. 1998; Lunn et al. 2002; electronic supplementary material, Table S7).

### 2.6 Elasticity analysis

We carried out elasticity analysis (de Kroon et al. 1986) to examine the relative effect of parameter selection on model prediction. We independently halved and doubled each model parameter in turn (intrinsic growth rate $\left(r_{\max }\right)$, number of individuals harvested $\left(C_{t}\right)$, current abundance estimate $\left(y_{t}\right)$, historical carrying capacity $(K)$, and observation error $\left(\sigma_{y}\right)$ ), and calculated elasticities $(e)$ of the $1850-2009$ population change, where higher $e$ means higher proportional change in the population (de Kroon et al. 1986; Benton and Grant 1999; Hunter, Moller, and Fletcher 2000). Y represents the population change caused by the altered parameter, $X$ :

$$
e=\frac{\% \Delta Y}{\% \Delta X}
$$

All analyses were carried out in the statistical software RStudio version 1.0.143 (RStudio Team 2015).

## 3. Results

### 3.1 Analysis of historical baselines

The median population change across the eight species for 1850 - 2009 was a $15 \%$ decrease ( $-0.1 \% / \mathrm{yr}$ ), whereas populations between $1970-2009$ showed a $4 \%$ increase $(0.1 \% / \mathrm{yr})$ (paired t -test: $\mathrm{t}=-3.036,1$ d.f. $=7, p=0.002, n=8$; Table 1, Figure 3a).
Choice of baseline year resulted in a switch from a downward population trend for the period 1850 - 2009 to an upward trend for 1970 - 2009 for four species (Arctic fox, bobcat, polar bear, beaver) (Figure 3b; Table S8; Figure S1). Six species exhibited a more severe annual rate of population change for the 1850-2009 period compared to trends derived from a 1970 baseline (Table 1; Figure 3b), with this pattern holding for five species when the annual rate of population change is considered (Table 1 ).

### 3.2 Single versus multiple causes of mortality

Analysis of the polar bear data that encompassed all recorded mortality events from 1970 onwards shows that an additional 294 (range $=-57$ to 538) individuals were killed in comparison to the number harvested for furs alone (electronic supplementary material, Table S7). This altered the polar bear population decline using the 1850 baseline from $22 \%$ based on fur harvest data alone to $41 \%$ using the IUCN/SSC data (Figure 4).

### 3.3 Elasticity analysis

Parameters ranked in order of lowest to highest elasticity (proportional change in the population) were observation error, carrying capacity, harvest data, current abundance estimate and intrinsic growth rate (Figure 5, Electronic supplementary material, Table S9). In other words, small changes to intrinsic growth rate and abundance estimates cause larger alterations to the model output. Species ranked in order of lowest to highest average elasticity for all informative priors were fisher, black bear, American badger, arctic fox, bobcat, polar bear, Canadian Lynx and beaver.

## 4. Discussion

Our study demonstrates that for eight species of Canadian mammals, choice of baseline year greatly affects our understanding of historic population change. Collectively, using an 1850 baseline year rather than 1970 significantly altered the population trend. Analysis of individual species demonstrated that deriving population change from the 1850 baseline resulted in four species shifting from a
population increase since 1970 to a population decrease of between 0 and $-22 \%$ since 1850, and the magnitude of annual population change becoming more severe for six species (Figure 3). Interestingly, the polar bear, the only species to be listed as Vulnerable on the IUCN Red List (Wiig et al. 2015), was one of the four species to show a shift in population trend. From 1850, the population declined, reflecting the polar bear's IUCN conservation status, whereas the trend from 1970 showed the population as increasing.

Population time-series data allow for the detection of declines before species reach critical status (Balmford and Bond 2005; Di Fonzo et al. 2016; Collen et al. 2011). However, few long-term population studies used data more than 100 years old (e.g., $15 \%$; Bonebrake et al. 2010). Biodiversity indicators that are reliant on such population time series data, such as the Living Planet Index (LPI), therefore often operate on baselines set to post-1950 (Bonebrake et al. 2010). At least for temperate systems, the LPI dataset may not date back far enough to detect often precipitous population declines which occurred prior to 1970 (Watson et al. 2005). For example, while some population recovery is observed in Europe since 1970 (Deinet et al. 2013), species are often recovering from declines which had reduced populations to a fraction of their historical population sizes by or prior to 1970. These short-term baselines are likely a result of the relatively recent advent of conservation biology in the 1970s and 1980s and corresponding emergence of long-term monitoring data for ecology and conservation (Collen et al. 2009).

In this study, we were able to model seven species currently listed as Least Concern on the IUCN Red List and not assessed under the Canadian Wildlife Species at Risk assessment (COSEWIC 2019). However, for five relatively common species: muskrat, marten, red fox, mink, and coyote that we collected harvest data for, a lack of recent population estimates at the regional or national scale prevented population modelling. Species are rarely subject to monitoring until declines are apparent and they may be of conservation concern (Bonebrake et al. 2010), while threatened species are often prioritised for monitoring, given limited financial resources and capacity (Gaston and Fuller 2008). As we are frequently witnessing population declines in common species, it is imperative that population monitoring also targets abundant or common species (Collen et al. 2011). This proactive approach enables early detection of declines, rather than a late reactive response when a species has already declined extensively, thus approaching extinction. This is of particular importance as abundant species play important parts in the functioning and maintenance of ecosystems (Winfree et al. 2015).

The strengths of using HBC data to estimate population change is the consistent unit over time (number of furs traded) and high temporal resolution (annual data), which overcome limitations oftentimes associated with historical records (Balmford and Bond 2005; Mcclenachan, Ferretti, and Baum 2012). While HBC data provides a very unique set of data, hunting statistics are available in many countries (e.g. Agetsuma 2018), and have a long tradition in regions such as Europe (Deinet et al. 2013; Hewitt
and Hewitt 2015). Hunting bag records were used in a recent study to analyse longterm population trends across a number of European countries for several game bird, ungulate and carnivore species, although the study only reached back as far as 1970 (Reimoser and Reimoser 2017). In the UK, the voluntary National Gamebag Census was formally established in 1961 but resulting records on game birds and predatory species extend back to 1900 for many species (Whitlock, Aebischer, and Reynolds 2003; Aebischer and Baines 2008). Models such as the one utilised in this study play an important role not just in deriving generalised trends, but also population estimates using such data repositories. Hunting statistics can then complement, or be used in tandem with, data from different sources such as transgenerational local ecological knowledge to obtain historical population baselines.

Despite our robust methods, population estimates from historical information such as harvest data are of lower quality than those derived from direct counts and current population monitoring, and uncertainty surrounding the estimates is inevitably greater. While some losses are not reported, resulting in a potential underestimate of the population (see methods 2.2), the spatial pattern of hunting that occurred throughout Canada in the past is likely to lead to an overestimate of hunting offtake of species. Hunting efforts saw a large westward expansion between 1783-1821, driven in large part by local depletion of beaver in the 'Canadian Shield' (Hope 2016; Figure 2). New areas such as the Red River Settlement, which was established in 1811, would have allowed access to previously unharvested subpopulations of mammals, and a boost to total harvest numbers. On the other hand, sources suggest that HBC was attempting to conserve beaver and bison in the 1820s (Colpitts 2017), presumably by enacting policies to help local population recovery, thus lowering total harvest. These local variations in harvest effort are not visible in our dataset, and the impact of uncertainty on our population estimates is illustrated by the mid-range elasticity of our model to a halving and doubling of harvest data (c) (Figure 5; Table S7). To some degree, our baseline of 1850 may help circumvent some of the previous geographical shifts or expansions in hunting effort. However, next steps should endeavour to account for spatial variation in hunting records over time by adding a spatially explicit component to the stock reduction analysis.

In addition to hunting, other drivers of population change are likely to impact our species, and focus on only a single cause of population offtake is likely to underestimate population trends over time. Substituting IUCN/SSC data on polar bear mortality via direct contact with humans into the final 40 years of our model changed the estimated decline from $25 \%$ (based on fur hunting data alone) to $41 \%$ (Figure 4). As well as providing hunting numbers, the IUCN/SSC polar bear data also includes 'individuals found dead'. This statistic includes mortality events which may be human-mediated or a result of natural causes, such as starvation from lack of sea ice. While hunting is a key human-mediated impact, it is but one of several sources of population decline facing mammals in North America (Brook, Sodhi, and Bradshaw 2008; Grooten and Almond 2018; Spooner, Pearson, and Freeman 2018).

Other anthropogenic drivers of population change such as habitat loss and the introduction of non-native species are not included in this analysis, again rendering our estimates conservative. For example, habitat loss affected the vast majority of threatened mammals in Canada, with direct human-caused mortality coming second (Imre and Derbowka 2009). Although modelling the impacts of all negative and positive anthropogenic effects on abundance is beyond the scope of this study, we can be fairly certain that these threats would play a role in determining the population size, intrinsic growth rates and carrying capacity within regions of Canada. As anthropogenic threats are dynamic (Wilcove et al. 1998), the degree of impact on the population will also alter over time. This highlights the need to quantify the impact of other threats which may influence these population parameters differentially over time (e.g. land use change altering carrying capacity) and incorporate these into baseline population models. One way of achieving this could be to allow carrying capacity K to vary across the time frame of our model in response to observed range contractions. In choosing a baseline for constructing historic population trends, we are ourselves guilty of ignoring what happened to our species prior to our chosen year of 1850. However, we recognize that the fur trade existed far back beyond this. Hunting for fur was carried out by Native Americans and European settlers alike; during the $17^{\text {th }}$ century, the French owned the monopoly of the Canadian fur trade and by 1717, HBC had set up six trading posts (Voorhis 1930). By 1850, the fur trade had impacted wildlife on the east coast; between 1860 and 1920 the sea mink (Neovison macrodon) reportedly went extinct (Mowat 2012; Black, Reading, and Savage 1998). While we use 1850 to demonstrate the importance of a historical baseline for as many species as possible, the term 'baseline' is not used here to imply a 'start' date, nor do we claim that one date will suffice. Rather, historical baselines should be viewed as a sliding window, and in conservation, it is important to move that window as far back as possible through history, to provide better context for species' current population status.

## 5. Conclusions

By failing to estimate historical baselines, we may miss the historical demise of populations which have been exploited by humans since at least the $18^{\text {th }}$ century in Europe and North America (Deinet et al. 2013), and adversely influence our perception of what constitutes species population norms. This may affect how scientists, decision makers and the general public perceive the growth of a population as a result of conservation action and species protection. While in many northern hemisphere regions, population recovery to an 1850 (or earlier) baseline may no longer be viable, due to the extensive anthropogenic land use change that has occurred in the interim, our current understanding of population recovery may focus on population sizes which are too small and could leave populations vulnerable to future threats or dependent on continued conservation action. We encourage the use of well-documented and quantifiable historical records in developing population baselines, thus establishing a broad temporal scale over which to analyse species
population trends. Armed with such data, we can improve our communication about population declines and set ambitious goals for realistically achievable population recovery (Akcakaya et al. 2018), make better-informed conservation management decisions, and improve our historical ecological awareness.

## Supporting Materials

All datasets supporting this article have been uploaded as part of the supplementary material.

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Tables and Figures
653 Table 1. Estimated percentage population change from 1850 and 1970 to 2009 for the eight modelled species. Mean population values are presented in bold and confidence intervals are presented in brackets.

| Species | 1850 <br> population | $1970$ <br> population | $2009$ <br> population | $1850-2009$ <br>  <br> annual) <br> population <br> loss or gain (\%) | 1970-2009 <br>  <br> annual) <br> population <br> loss or gain (\%) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Arctic fox | 133,000 | 132,000 | 133,000 | 0 (0) | 1 (0.02) |
| Canadian lynx | 262,000 | 258,000 | 290,000 | 11 (0.06) | 12 (0.32) |
| Beaver | 4,730,000 | 3,730,000 | 4,440,000 | -6 (-0.04) | 19 (0.49) |
| Bobcat | 50,300 | 44,100 | 47,000 | -7 (-0.04) | 7 (0.17) |
| Polar bear | 20,300 | 13,900 | 15,800 | -22 (-0.14) | 14 (0.35) |
| Black bear | 831,000 | 414,000 | 390,000 | -53 (-0.33) | -6 (-0.15) |
| Fisher | 167,000 | 157,000 | 7,000 | -96 (-0.60) | -96 (-2.45) |
| American badger | 518,000 | 175,000 | 83,800 | -84 (-0.53) | -52 (-1.34) |



Figure 1. Schematic of hypothetical population trends highlighting the benefits of establishing a historical baseline through (A) providing better context on the extent of decline, thus allowing for better population recovery scenarios when advising on recovery targets (blue arrows signify extent of known decline), (B) identifying a trend through different time series lengths (represented by blue arrows) and discriminating between true decreasing trends and misattributed trends caused by population cycles, and (C) estimating the impact on populations from known drivers of decline captured through use of historical baselines.


Figure 2. The approximate locations of all Hudson's Bay Company trading posts that were operating in 1927 in North America, adapted from Elton and Nicholson (1942a).


Figure 3. Percentage change in population estimates using two different baseline years: 1850-2009 and 1970-2009 for (A) species cumulatively (t-test: $p<0.05 ; 1970$ : $4 \%, 1850:-14.5 \%$ medians $\pm$ S.E, $n=8$ ), and (B) species-specific population estimates.


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Figure 4. Population trajectories for polar bear, using, from 1970, (A) Canadian government annual fur harvest data and (B) IUCN/SSC statistics on number of polar bears annually killed in Canada. Pink bars are the annual fur harvest (right-hand axis), the blue solid line and blue dashed lines are the population projection and the $95 \%$ median confidence intervals respectively; the current Canada-wide population estimate is shown by the red dots (left-hand axis).
arameter alteration

- Ct doubled
- Ct halved
- K lower bound (0 value)
-- K upper bound doubled
- original estimate
- rmax doubled
- Standard deviation (0.9 value)
- oy doubled
- oy halved

Figure 5. Elasticity analysis for each species, showing how population change between 1850-2009 altered when each parameter was doubled (+50) and halved (-50) for number of individuals caught ( $C_{t}$, orange lines); carrying capacity $(K)$ lower bound and carrying capacity upper bound (blue lines); original SSRA estimate (black line); intrinsic growth rate ( $r_{\max }$, green lines); standard deviation altered to 0.9 (grey line); abundance estimate(s) ( $y_{t}$; purple lines); observation error ( $\sigma_{\mathrm{y}}$, pink lines).

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## Declaration of Interest

The authors have no competing interests to declare.

## Authors' contributions

Amy Collins: Conceptualization, Methodology, Software, Formal analysis, Writing- Original Draft, Visualization. Monika Böhm: Resources, Writing - Review \& Editing, Supervision.
Ben Collen: Conceptualization, Validation, Writing - Review \& Editing, Supervision.

## Supplementary Material for

Reconstructing historical population baselines for hunted mammals

## Tables

Table S1. Data availability for 25 mammal species for which Hudson's Bay Company data exists. The year highlighted in red represents the first year that harvest data is available ( $\mathrm{BC}=$ British Columbia).

| Species | Harvest datasets |  |  |  |  |  |  | Current estimate yt |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Common name | Poland <br> (1892) <br> 1751-1889 | Jones <br> (1914) <br> 1890-1909 | Novak <br> (1987) <br> 1919-1969 | Fur <br> Statistics <br> Canada <br> (2010) <br> 1970-2009 | Other harvest Data | Extra interpolated years ${ }^{1}$ |  |
| Ursus americanus | Black (and brown) bear | $1751$ | $\checkmark$ | $\checkmark$ | $\checkmark$ |  |  | $\checkmark$ |
| Lynx canadensis | Canadian Lynx | $\checkmark$ | $\checkmark$ | $\checkmark$ | $\checkmark$ | Elton and Nicholson (1942) 1735-1750 | 1942 | $\checkmark$ |
| Martes pennanti | Fisher | $1766$ | $\checkmark$ | $\checkmark$ | $\checkmark$ |  |  | Extrapolated from BC |
| Ursus maritimus | Polar bear | $1751$ | $\checkmark$ | $\checkmark$ | $\checkmark$ |  |  | $\checkmark$ |
| Vulpes lagopus | Arctic fox | $1751$ | $\checkmark$ | $\checkmark$ | $\checkmark$ |  |  | $\checkmark$ |
| Taxidea taxus | American Badger | $1842$ | $\checkmark$ | $\checkmark$ | $\checkmark$ | Gobal <br> Population <br> Dynamics <br> Database <br> (2010) <br> 1891-1908 | 1908-1910 | $\checkmark$ |
| Castor canadensis | Beaver | $\checkmark$ | $\checkmark$ | $\checkmark$ | $\checkmark$ | Carlos \& | 1815, 1827- | Extrapolated |



|  | Deer | $\checkmark$ | $\boxtimes$ | $\boxtimes$ | $\checkmark$ |
| :--- | :--- | :--- | :---: | :---: | :---: |
| Ovibos moschatus | Muskox | $\boxtimes$ | $\checkmark$ | $\boxtimes$ | $\checkmark$ |
|  | Rabbit | $\checkmark$ | $\boxtimes$ | $\boxtimes$ | $\checkmark$ |
| Mephitis mephitis | Skunk | $\boxtimes$ | $\checkmark$ | $\boxtimes$ | $\checkmark$ |
|  | Swan | $\checkmark$ | $\boxtimes$ | $\boxtimes$ | $\checkmark$ |
| Mustela erminea | Stoat | $\boxtimes$ | $\checkmark$ | $\boxtimes$ | $\checkmark$ |

${ }^{1}$ in addition to 1910-1918 and 2002, see methods in the main manuscript

Table S2. Hudson's Bay Company harvest data for the eight species modelled in our analysis. HBC fur harvest data may report the year the furs were caught $(y)$; the year when the furs were sent to HBC headquarters $(y+1)$; or the year the furs were sold at the London auctions $(y+2)$ (Powell et. al. 2003). To ensure consistency across both datasets, we backdated the data to reflect the number of furs caught in year $y$, by backdating the data from Poland (1892) by one year and that of Jones (1914) by two years, as described in Elton \& Nicholson (1942).

| Year | Arctic fox | American | Beaver | Species Harvest Data |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Black Bear | Bobcat | Canadian Lynx | Fisher | Polar Bear |  |  |  |  |
| 1850 | 854 | 1471 | 62277 | 7106 | 243 | 8519 | 5967 | 97 |
| 1851 | 4012 | 1710 | 52491 | 7381 | 222 | 5361 | 5861 | 101 |
| 1852 | 4104 | 956 | 60691 | 6244 | 135 | 4552 | 4933 | 85 |
| 1853 | 1406 | 900 | 62914 | 9139 | 381 | 5682 | 4901 | 125 |
| 1854 | 10413 | 1240 | 72425 | 9218 | 330 | 11358 | 5210 | 126 |
| 1855 | 5014 | 999 | 76825 | 8070 | 214 | 23362 | 5563 | 110 |
| 1856 | 2123 | 1185 | 86414 | 8019 | 208 | 31642 | 5957 | 110 |
| 1857 | 1592 | 1369 | 94058 | 8800 | 189 | 33757 | 6950 | 120 |
| 1858 | 3398 | 1773 | 106797 | 8032 | 143 | 23226 | 7197 | 110 |
| 1859 | 5111 | 1213 | 107745 | 7372 | 134 | 15178 | 5853 | 101 |
| 1860 | 2828 | 1091 | 105562 | 8101 | 115 | 7272 | 5980 | 111 |
| 1861 | 3394 | 1642 | 109636 | 7467 | 164 | 4448 | 6053 | 102 |
| 1862 | 12324 | 1295 | 127674 | 7770 | 75 | 4926 | 5424 | 106 |
| 1863 | 4854 | 1562 | 118118 | 7236 | 63 | 5437 | 4953 | 99 |
| 1864 | 5955 | 1235 | 155880 | 8809 | 117 | 16498 | 4605 | 121 |
| 1865 | 5446 | 618 | 150192 | 7499 | 83 | 35971 | 4804 | 103 |
| 1866 | 2554 | 1644 | 145654 | 6825 | 94 | 76556 | 6311 | 93 |
| 1867 | 12212 | 1781 | 158110 | 8542 | 89 | 68392 | 7477 | 117 |
| 1868 | 4677 | 2288 | 129039 | 8305 | 68 | 37447 | 7959 | 114 |
| 1869 | 1820 | 1986 | 173181 | 8471 | 82 | 15686 | 6743 | 116 |
| 1870 | 2842 | 2274 | 174461 | 8452 | 46 | 7942 | 7072 | 116 |


| 1871 | 7415 | 2786 | 157764 | 8060 | 24 | 5123 | 3639 | 110 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1872 | 5375 | 1512 | 105369 | 7329 | 28 | 7106 | 3539 | 100 |
| 1873 | 6127 | 1870 | 139393 | 7022 | 189 | 11250 | 3578 | 96 |
| 1874 | 4381 | 2280 | 129976 | 7697 | 83 | 18774 | 3263 | 105 |
| 1875 | 5347 | 2273 | 126959 | 7440 | 40 | 30508 | 3338 | 102 |
| 1876 | 24641 | 2474 | 145706 | 7313 | 10 | 42834 | 5461 | 100 |
| 1877 | 6018 | 2031 | 147263 | 7689 | 10 | 27345 | 6132 | 105 |
| 1878 | 2335 | 2866 | 132099 | 5869 | 2 | 17834 | 4216 | 80 |
| 1879 | 4412 | 1867 | 120836 | 8414 | 24 | 15386 | 5059 | 115 |
| 1880 | 5777 | 1428 | 119698 | 7911 | 6 | 9443 | 5143 | 108 |
| 1881 | 5923 | 1499 | 118728 | 11035 | 19 | 7599 | 4640 | 151 |
| 1882 | 6537 | 746 | 104459 | 5439 | 10 | 8061 | 3820 | 74 |
| 1883 | 2819 | 1330 | 119549 | 10618 | 24 | 27187 | 4200 | 145 |
| 1884 | 3298 | 1473 | 102589 | 8271 | 10 | 51511 | 1041 | 113 |
| 1885 | 4187 | 749 | 83589 | 8166 | 18 | 74050 | 4510 | 112 |
| 1886 | 13243 | 1109 | 102745 | 9942 | 33 | 78773 | 6165 | 136 |
| 1887 | 9628 | 777 | 33061 | 9474 | 18 | 33899 | 5408 | 130 |
| 1888 | 2918 | 1301 | 73355 | 11558 | 16 | 18886 | 6557 | 158 |
| 1889 | 3763 | 2445 | 64246 | 10371 | 14 | 11520 | 5683 | 83 |
| 1890 | 9709 | 4000 | 55000 | 13289 | 13 | 8352 | 5208 | 130 |
| 1891 | 4759 | 2600 | 56000 | 11073 | 5 | 8660 | 4828 | 90 |
| 1892 | 3265 | 3000 | 45000 | 8834 | 7 | 12902 | 4044 | 134 |
| 1893 | 5017 | 2000 | 45000 | 9810 | 29 | 20331 | 38631 | 81 |
| 1894 | 6748 | 2200 | 50000 | 9557 | 15 | 36853 | 4169 | 128 |
| 1895 | 3542 | 2000 | 50000 | 10348 | 50 | 56407 | 4805 | 77 |
| 1896 | 3274 | 1100 | 42000 | 10138 | 32 | 39437 | 5247 | 141 |
| 1897 | 6742 | 1200 | 34000 | 9903 | 27 | 26761 | 4964 | 130 |
| 1898 | 3642 | 1300 | 44000 | 10034 | 67 | 15185 | 5042 | 118 |


| 1899 | 2953 | 600 | 41000 | 8607 | 41 | 4473 | 3454 | 58 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1900 | 8583 | 1100 | 43000 | 7875 | 5 | 5781 | 3716 | 170 |
| 1901 | 10841 | 700 | 45000 | 7171 | 4 | 9117 | 3235 | 96 |
| 1902 | 5622 | 500 | 35000 | 6725 | 5 | 19267 | 2590 | 55 |
| 1903 | 4707 | 500 | 30000 | 5077 | 3 | 36116 | 2095 | 54 |
| 1904 | 6438 | 500 | 55000 | 5536 | 2 | 58850 | 3020 | 149 |
| 1905 | 11539 | 300 | 35000 | 4612 | 2 | 61478 | 4022 | 138 |
| 1906 | 6849 | 100 | 32000 | 4488 | 1 | 36300 | 4701 | 60 |
| 1907 | 2082 | 100 | 35000 | 4439 | 1 | 9704 | 3600 | 93 |
| 1908 | 4831 | 138 | 40651 | 5032 | 1 | 3410 | 2525 | 71 |
| 1909 | 14805 | 190 | 47213 | 5348 | 2 | 3774 | 2310 | 82 |
| 1910 | 15094 | 262 | 54836 | 5251 | 3 | 6149 | 2679 | 82 |
| 191 | 15388 | 362 | 63689 | 5555 | 6 | 10020 | 3107 | 99 |
| 1912 | 15689 | 499 | 73971 | 5876 | 10 | 16327 | 3604 | 109 |
| 1913 | 15995 | 688 | 85913 | 6216 | 18 | 26604 | 4180 | 120 |
| 1914 | 16307 | 948 | 99783 | 6576 | 31 | 43349 | 4848 | 132 |
| 1915 | 16625 | 1308 | 115893 | 6956 | 55 | 31998 | 5623 | 145 |
| 1916 | 16949 | 1804 | 134603 | 7359 | 95 | 23619 | 6522 | 160 |
| 1917 | 17280 | 2487 | 156334 | 7784 | 164 | 17434 | 7565 | 176 |
| 1918 | 17617 | 3430 | 181574 | 8235 | 285 | 12869 | 8774 | 194 |
| 1919 | 17961 | 4730 | 210888 | 8771 | 495 | 9499 | 10176 | 213 |
| 1920 | 21537 | 930 | 164656 | 7786 | 859 | 6509 | 4866 | 282 |
| 1921 | 41082 | 1627 | 232134 | 9511 | 3583 | 11673 | 5689 | 378 |
| 1922 | 77648 | 2773 | 175275 | 7368 | 1129 | 17317 | 3976 | 313 |
| 1923 | 34973 | 5147 | 169172 | 6999 | 3279 | 26437 | 4158 | 412 |
| 1924 | 44535 | 9298 | 151913 | 8429 | 3941 | 29608 | 4230 | 456 |
| 1925 | 35397 | 13373 | 111707 | 6173 | 3324 | 33054 | 5899 | 330 |
| 1926 | 51552 | 22073 | 100364 | 6374 | 3403 | 28706 | 7893 | 203 |


| 1927 | 34099 | 33516 | 74338 | 6857 | 1493 | 21369 | 8641 | 388 |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1928 | 18687 | 34761 | 67043 | 6828 | 1728 | 11604 | 6606 | 304 |
| 1929 | 38028 | 14793 | 47715 | 6588 | 827 | 7621 | 4274 | 331 |
| 1930 | 72176 | 10039 | 51313 | 4634 | 464 | 7976 | 3282 | 261 |
| 1931 | 67924 | 4964 | 65276 | 2754 | 800 | 8454 | 2739 | 130 |
| 1932 | 33582 | 3159 | 71699 | 2241 | 1654 | 11932 | 2530 | 73 |
| 1933 | 61782 | 3047 | 59199 | 1416 | 1917 | 16799 | 3171 | 27 |
| 1934 | 69033 | 1225 | 50175 | 1123 | 2218 | 22014 | 3728 | 43 |
| 1935 | 46151 | 157 | 44600 | 1025 | 1884 | 22456 | 4624 | 59 |
| 1936 | 22625 | 141 | 55759 | 1885 | 1565 | 17539 | 5237 | 49 |
| 1937 | 56879 | 203 | 54148 | 1642 | 1093 | 10538 | 3505 | 150 |
| 1938 | 57007 | 3237 | 64086 | 1626 | 1125 | 8109 | 3399 | 115 |
| 1939 | 33111 | 4663 | 78659 | 1058 | 1184 | 7473 | 2886 | 150 |
| 1940 | 48980 | 8240 | 90123 | 1056 | 1138 | 6684 | 2212 | 106 |
| 1941 | 63654 | 11478 | 106176 | 1218 | 2124 | 7109 | 3408 | 91 |
| 1942 | 74637 | 7575 | 102241 | 1032 | 2117 | 8512 | 2165 | 65 |
| 1943 | 30716 | 11212 | 130764 | 1448 | 2214 | 10191 | 3303 | 95 |
| 1944 | 18122 | 5708 | 128999 | 2344 | 2200 | 12329 | 3631 | 95 |
| 1945 | 27585 | 6373 | 153899 | 1145 | 1585 | 9338 | 4141 | 202 |
| 1946 | 68363 | 2090 | 127622 | 1150 | 1365 | 8147 | 4064 | 150 |
| 1947 | 55960 | 1034 | 135629 | 827 | 1265 | 6582 | 2788 | 246 |
| 1948 | 33460 | 685 | 161926 | 579 | 476 | 4110 | 4390 | 422 |
| 1949 | 20019 | 1125 | 157416 | 760 | 781 | 3734 | 2698 | 297 |
| 1950 | 53141 | 702 | 180817 | 410 | 649 | 9662 | 3690 | 377 |
| 1951 | 54393 | 508 | 222932 | 330 | 662 | 7324 | 5274 | 420 |
| 1952 | 4149 | 215 | 224606 | 598 | 501 | 13099 | 5531 | 465 |
| 1953 | 36853 | 268 | 242452 | 437 | 490 | 11325 | 5794 | 458 |
| 1954 | 82626 | 249 | 320389 | 324 | 345 | 14427 | 6790 | 530 |


| 1955 | 31999 | 271 | 282036 | 319 | 1404 | 9988 | 6324 | 454 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| 1956 | 28565 | 395 | 280671 | 578 | 512 | 8748 | 5076 | 445 |
| 1957 | 32170 | 663 | 341674 | 775 | 564 | 9506 | 5720 | 558 |
| 1958 | 26752 | 348 | 328584 | 493 | 778 | 14165 | 4850 | 413 |
| 1959 | 14632 | 1446 | 344766 | 411 | 1336 | 40408 | 6462 | 544 |
| 1960 | 52245 | 827 | 399459 | 404 | 1326 | 42016 | 6206 | 575 |
| 1961 | 45769 | 658 | 386823 | 2256 | 855 | 47625 | 5863 | 497 |
| 1962 | 9934 | 388 | 436780 | 715 | 1070 | 51376 | 6254 | 477 |
| 1963 | 32618 | 409 | 463837 | 683 | 1133 | 36197 | 8364 | 482 |
| 1964 | 41038 | 395 | 415261 | 1211 | 1533 | 24534 | 7950 | 564 |
| 1965 | 11726 | 792 | 372635 | 2482 | 3305 | 14583 | 8216 | 624 |
| 1966 | 34315 | 1163 | 371533 | 1938 | 3658 | 13038 | 6856 | 724 |
| 1967 | 29791 | 1251 | 420437 | 1777 | 2483 | 15848 | 5535 | 452 |
| 1968 | 20299 | 1215 | 437875 | 3224 | 3266 | 20677 | 7627 | 404 |
| 1969 | 7477 | 4084 | 433408 | 3200 | 4118 | 37477 | 8146 | 326 |
| 1970 | 26301 | 2014 | 355379 | 2007 | 3408 | 42365 | 6637 | 361 |
| 1971 | 33788 | 2121 | 375213 | 2522 | 3837 | 53589 | 8278 | 389 |
| 1972 | 10265 | 5170 | 452275 | 3008 | 3682 | 53400 | 13798 | 472 |
| 1973 | 53623 | 5134 | 431071 | 4261 | 4129 | 35372 | 12566 | 546 |
| 1974 | 32120 | 3626 | 357732 | 3585 | 3425 | 20648 | 10163 | 548 |
| 1975 | 26913 | 5124 | 334924 | 3531 | 3103 | 13162 | 8698 | 406 |
| 1976 | 36840 | 6834 | 404625 | 3402 | 3459 | 15132 | 9664 | 522 |
| 1977 | 33262 | 5279 | 397125 | 3170 | 3790 | 21131 | 8798 | 523 |
| 1978 | 25853 | 7800 | 446416 | 4109 | 4499 | 29987 | 9771 | 515 |
| 1979 | 35697 | 7736 | 602044 | 4710 | 4494 | 34366 | 14725 | 371 |
| 1980 | 40828 | 4013 | 522966 | 3872 | 2499 | 34502 | 14935 | 427 |
| 1981 | 18291 | 3965 | 382893 | 2175 | 2773 | 39274 | 16413 | 363 |
| 1982 | 14532 | 4333 | 335711 | 2464 | 2300 | 29533 | 21005 | 227 |


| 1983 | 16096 | 3028 | 323877 | 2340 | 2128 | 13445 | 17931 | 355 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1984 | 22952 | 3723 | 371685 | 2411 | 2128 | 8625 | 14483 | 296 |
| 1985 | 6493 | 2036 | 424086 | 2385 | 1861 | 6853 | 15537 | 351 |
| 1986 | 8394 | 2280 | 505996 | 2879 | 1749 | 6953 | 15020 | 277 |
| 1987 | 18663 | 2107 | 464992 | 3330 | 1343 | 6574 | 12664 | 288 |
| 1988 | 2524 | 1068 | 267427 | 1820 | 952 | 8265 | 9183 | 360 |
| 1989 | 2266 | 648 | 222605 | 3169 | 537 | 9977 | 7759 | 380 |
| 1990 | 1112 | 574 | 179962 | 2095 | 583 | 7579 | 8831 | 271 |
| 1991 | 3190 | 933 | 219764 | 1901 | 436 | 11542 | 15381 | 279 |
| 1992 | 3946 | 686 | 185965 | 2647 | 628 | 7180 | 13377 | 180 |
| 1993 | 10020 | 758 | 244561 | 2507 | 727 | 4713 | 13105 | 117 |
| 1994 | 11434 | 863 | 327229 | 2992 | 1066 | 4907 | 14578 | 116 |
| 1995 | 1999 | 884 | 243724 | 2807 | 976 | 2819 | 11806 | 57 |
| 1996 | 6106 | 646 | 320358 | 2224 | 1320 | 5171 | 15351 | 102 |
| 1997 | 6572 | 731 | 314804 | 2140 | 1457 | 6873 | 20253 | 101 |
| 1998 | 4358 | 397 | 266146 | 1984 | 1452 | 6148 | 15223 | 76 |
| 1999 | 3674 | 353 | 215246 | 2015 | 1801 | 8573 | 16638 | 134 |
| 2000 | 5897 | 496 | 221118 | 2918 | 1769 | 9361 | 16109 | 39 |
| 2001 | 7398 | 490 | 260421 | 3406 | 2070 | 11328 | 23456 | 28 |
| 2002 | 5347 | 849 | 224658 | 3250 | 2004 | 12341 | 21687 | 59 |
| 2003 | 3864 | 1471 | 193807 | 3102 | 1941 | 11896 | 20052 | 126 |
| 2004 | 1311 | 486 | 190930 | 2674 | 1632 | 9788 | 19345 | 76 |
| 2005 | 1430 | 774 | 198304 | 2289 | 1517 | 8445 | 19771 | 7 |
| 2006 | 3505 | 1063 | 210423 | 2183 | 1827 | 8455 | 19675 | 83 |
| 2007 | 2610 | 982 | 147685 | 2213 | 1866 | 6630 | 17151 | 65 |
| 2008 | 2520 | 624 | 152782 | 2008 | 2192 | 9216 | 17575 | 102 |
| 2009 | 1003 | 512 | 139220 | 2055 | 1770 | 7490 | 16373 | 259 |

Table S3. Median population growth rate $r_{\text {max }}$, standard deviation, and original referenced $r_{\text {max }}$ values used for the eight species' prior probability in the Stochastic Stock Reduction Analysis.

| Species Common <br> Name | Species | Median $\mathrm{R}_{\text {max }}$ | SD | $\mathrm{R}_{\text {max }}$ | Source |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Arctic Fox | Alopex lagopus | 1.43 | 1.077821878 | 2.64 | Hutchings et al. (2012) |
|  |  |  |  | 1.43 | Hennemann (1983) |
|  |  |  |  | 0.49 | The Global Population Dynamics Database (GPDD) in Fagan et al. (2001) |
| American Badger | Taxidea taxus | 0.678 | 0.405862253 | 0.38 | Hutchings et al. (2012) |
|  |  |  |  | 0.976 | Fagan et al (2013) |
|  |  |  |  | 1.01 | Thompson (1987) |
|  |  |  |  | 0.22 | GPDD in Fagan et al. (2001) |
| Beaver | Castor canadensis | 0.47 | 0.056047599 | 0.47 | GPDD in Fagan et al. (2001) |
|  |  |  |  | 0.442 | Lancia and Bishir (1985) |
|  |  |  |  | 0.55 | Runge (1999) |
| Black Bear | Ursus americanus | 0.23 | 0.125989998 | 0.23 | Hutchings et al. (2012) |
|  |  |  |  | 0.197 | Fagan et al (2013) |
|  |  |  |  | 0.43 | GPDD in Fagan et al. (2001) |
| Bobcat | Lynx rufus | 0.62 | 0.410121933 | 0.91 | Hutchings et al. (2012) |
|  |  |  |  | 0.33 | GPDD in Fagan et al. (2001) |
| Canadian Lynx | Lynx canadensis | 0.855 | 0.111015765 | 0.855 | Tanner (1975) |
|  |  |  |  | 1.012 | Tanner (1975) |
|  |  |  |  | 0.26 | GPDD in Fagan et al. (2001) |
| Fisher | Martes pennanti | 0.428 | 0.152879315 | 0.536 | Fagan et al 2013 [11] |
|  |  |  |  | 0.32 | GPDD in Fagan et al. (2001) |
| Polar Bear | Ursus maritimus | 0.06 | 0.202262775 | 0.0603 | http://polarbearfeed.etiennebenson.com/detail/50/None/4/ |
|  |  |  |  | 0.0055 | Taylor et al. (2005) |
|  |  |  |  | 0.38 | GPDD in Fagan et al. (2001) |

Table S4. Current population estimates $\left(y_{t} ; 1979-2013\right)$ and data source.

| Species Common Name | Species | Population estimate(s) | Year of estimate | Source |
| :---: | :---: | :---: | :---: | :---: |
| Arctic Fox | Alopex lagopus | 100,000 | 2004 | Sillero-Zubiri, Hoffman <br> \& Macdonald (2004) |
| American Badger | Taxidea taxus | 31,225 | 2002 | Scobie (2002) |
| Beaver | Castor canadensis | 3,550,000 | 1979 |  |
| Black Bear | Ursus americanus | 337,200 | 1989 | Williamson (2002) |
|  |  | 369,500 | 1992 |  |
|  |  | 436,000 | 1996 |  |
|  |  | 434,400 | 2001 | Hristienko \& McDonald (2007) |
| Bobcat | Lynx rufus | 59,832 | 2008 |  |
| Canadian Lynx | Lynx canadensis | 275,000 | 2003 | Poole (2003) |
| Fisher | Martes pennanti | 8,131 | 1999 | Weir (2000) |
| Polar Bear | Ursus maritimus | 12,700 | 1995 | Taylor \& Lee (1995) |
|  |  | 15,000 | 2002 |  |
|  |  | 15,500 | 2008 |  |

Table S5. Selection criteria used for allocating the proportion of the total error term, $k$, to the observation error, $\sigma_{\mathrm{y}}$, based on the source and uncertainty associated with the data, with province-wide extrapolation of population size assigned the highest proportion. The remaining total error term is attributed to the process error, $\mathrm{w}_{\mathrm{t}}$.

Proportion of the
total error term
0.3

Selection criteria
Single or multiple population estimates taken from a scientific journal/published article. Associated error or uncertainty surrounding the estimate(s) is recorded and small.
Single population estimate taken from a published article or published report and/or large associated error surrounding the estimate.
State-wide extrapolations to the entire current range required to obtain the current abundance.

Table S6. Upper and lower bound calculated for carrying capacity $(K)$ priors.

| Species Common Name | Species | Lower bound K | Upper bound K | Density estimate per $\mathrm{km}^{2}$ | Historical range estimate $\mathrm{km}^{2}$ (Seton Vol II 1929 [17] unless stated otherwise) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Arctic Fox | Alopex lagopus | 94,239 | 1,366,458 | 0.02-0.2 (Angerbjörn et al. 1999) | 4,711,926 |
| American Badger | Taxidea taxus | 504,089 | 3,780,666 | 0.8 (Goodrich \& Buskirk 1998) - 6 Messick \& Hornocker 1981) | 630,111 |
| Beaver | Castor canadensis | 2,554,444 | 352,513,327 | 0.4 (Feldhamer, <br> Thompson \& Chapman 2003) - 55.2 (Naiman, Johnston \& Kelley 1988) | 6,386,110 |
| Black Bear | Ursus americanus | 773,845 | 3,009,398 | 0.09-0.35 (McLean \& Pelton 1994) | 8,598,280 Pelton \& Coley 1999) |
| Bobcat | Lynx rufus | 9,454 | 55,568 | 0.09-0.529 (Roberts \& Crimmins 2010) | 105,042.7 |
| Canadian Lynx | Lynx canadensis | 115,500 | 2,598,750 | 0.02-0.45 (Sunquist \& Sunquist 2002) | 5,775,000 |
| Fisher | Martes pennanti | 182,786 | 1,389,175 | $\begin{aligned} & 0.05-0.38 \text { Powell et al. } \\ & \text { 2003) } \end{aligned}$ | 3,655,724 |
| Polar Bear | Ursus maritimus | 2,700 | 49,500 | 0.001 (Taylor \& Lee 1995) - 0.018 (Derocher 1998) | 2,701,800 |

Table S7. Number of polar bears killed for fur versus number killed from all major pressures from 1970 to 2008.
year
IUCN data - all anthropogenic pressures

Canadian government data single threat, fur harvest

Extra number of individuals killed from all pressures

| 1970 | 362 | 361 | 1 |
| :--- | :--- | ---: | ---: |
| 1971 | 368 | 389 | -21 |
| 1972 | 415 | 472 | -57 |
| 1973 | 548 | 546 | 2 |
| 1974 | 532 | 548 | -16 |
| 1975 | 476 | 406 | 70 |
| 1976 | 499 | 522 | -23 |
| 1977 | 540 | 523 | 17 |
| 1978 | 629 | 515 | 114 |
| 1979 | 598 | 371 | 227 |
| 1980 | 668 | 427 | 241 |
| 1981 | 663 | 363 | 300 |
| 1982 | 680 | 227 | 453 |
| 1983 | 694 | 355 | 339 |
| 1984 | 690 | 296 | 394 |
| 1985 | 645 | 351 | 294 |
| 1986 | 632 | 277 | 355 |
| 1987 | 600 | 288 | 312 |
| 1988 | 599 | 360 | 239 |
| 1989 | 648 | 380 | 268 |
| 1990 | 632 | 271 | 361 |
| 1991 | 572 | 279 | 293 |
| 1992 | 609 | 180 | 429 |


| 1993 | 567 | 117 | 450 |
| :---: | :---: | :---: | :---: |
| 1994 | 478 | 116 | 362 |
| 1995 | 511 | 57 | 454 |
| 1996 | 472 | 102 | 370 |
| 1997 | 529 | 101 | 428 |
| 1998 | 471 | 76 | 395 |
| 1999 | 482 | 134 | 348 |
| 2000 | 530 | 39 | 491 |
| 2001 | 453 | 28 | 425 |
| 2002 | 512 | 59 | 453 |
| 2003 | 495 | 126 | 369 |
| 2004 | 529 | 76 | 453 |
| 2005 | 545 | 7 | 538 |
| 2006 | 514 | 83 | 431 |
| 2007 | 577 | 65 | 512 |
| 2008 | 506 | 102 | 404 |
|  |  |  | 256 |

Table S8. Population change estimated from the SSRA model for each baseline scenario.

| Species | Population change (\%) |  |
| :---: | :---: | :---: |
| Baseline | $\mathbf{1 8 5 0}$ | $\mathbf{1 9 7 0}$ |
| Arctic fox | 0 | 1 |
| American Badger | -84 | -52 |
| Beaver | -6 | 19 |
| Black bear | -53 | -6 |
| Bobcat | -7 | 7 |
| Fisher | -96 | -96 |
| Canadian Lynx | 11 | 12 |
| Polar bear | -22 | 14 |

Table S9. Elasticities of species-specific population change (1850-2009) with respect to parameter alterations.

| Parameter | Magnitude of altered value | Arctic fox | American Badger | Beaver | Black bear | Bobcat | Fisher | Canadian Lynx | Polar bear |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Harvest data | Double | 0.05 | 0.07 | 0.34 | 0.05 | 0.27 | -0.03 | 0.68 | 0.55 |
|  | Half | 0.04 | 1.00 | 0.57 | 0.25 | 0.97 | -0.05 | 1.29 | 0.94 |
| Upper bound carrying capacity | Double | -0.01 | 0.02 | -0.03 | 0.01 | -0.06 | -0.04 | 0.00 | 0.02 |
|  | Half | 0.02 | -0.06 | -0.07 | 0.01 | -0.69 | -0.07 | 0.05 | 0.76 |
| Lower bound carrying capacity | Zero | 0.01 | -0.05 | 0.03 | 1.07 | 0.06 | -0.01 | -0.01 | -0.02 |
| Observation error | Double | 0.00 | -0.02 | 0.05 | -0.03 | -0.07 | -0.01 | -0.02 | -0.03 |
|  | Half | -0.02 | 0.08 | 0.10 | -0.01 | 0.11 | 0.00 | 0.02 | -0.09 |
| Current population estimate Intrinsic growth rate | Double | 0.00 | -0.03 | -0.23 | -0.52 | -0.12 | 0.01 | -0.32 | -0.27 |
|  | Half | 1.37 | 0.03 | -1.17 | -0.90 | -0.86 | -0.08 | -2.42 | -3.68 |
|  | Double | -0.01 | -0.49 | -0.28 | -0.03 | -0.24 | 0.01 | -0.51 | -0.34 |
|  | Half | 0.03 | -0.06 | -4.57 | 0.00 | -0.97 | 0.18 | -3.60 | -1.91 |










Figure S1. Modelled historical population projections using the pre-1850 baseline for A) American badger, B) arctic fox, C) beaver, D) black bear, E) bobcat, F) Canadian lynx, G) marten, H) polar bear. Pink bars are the annual fur harvest (right-hand axis), the blue solid line and blue
dashed lines are the population projection and the $95 \%$ median confidence intervals respectively, and the current Canada-wide population estimate is shown by the red dots (left-hand axis).

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