DEMOGRAPHY AND POPULATION VIABILITY OF POLAR BEARS IN KANE BASIN, NUNAVUT AND GREENLAND

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Abstract: We estimated demographic parameters and harvest risks for a population of high arctic polar bears (Ursus maritimus) inhabiting Kane Basin, Canada and Greenland, from 1992 to 1997. Our demographic analysis included a detailed assessment of age- and sex-specific survival and recruitment from 272 marked polar bears, using information contained within the standing age distribution of captures and mark-recapture analysis. We constructed estimates of survival and abundance from capture-recapture and recovery (harvest) data using a Barker model formulation implemented in program MARK. Model likelihood was based on recapture events of marked animals and was used to define a series of models for survival and recapture probabilities expressed as functions of covariates such as sex, age, and time. We incorporated demographic parameters and their variances into a harvest risk analysis designed to consider demographic, process, and sampling uncertainty in generating likelihoods of persistence (i.e., a stochastic, harvested Population Viability Analysis [PVA]).

Key Words: demography, mark-recapture, polar bear, Population Viability Analysis (PVA), program MARK, harvest

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Introduction

Polar bears (*Ursus maritimus*), like many long-lived animals, are susceptible to overharvest. All previous declines in polar bear populations in Canada, for example, can be attributed to unsustainable hunting (e.g., Western Hudson Bay [Derocher and Stirling 1995]; Viscount-Melville Sound [Taylor et al. 2002]; M'Clintock Channel [M. K. Taylor, unpubl. Data]). Late age at maturity, small litter sizes, and long interbirth intervals maintain low intrinsic rates of increase for the species. Because of this, all populations of polar bears in Canada are classified as being of 'special concern' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002).

Polar bears inhabiting areas north of 79° latitude, however, may be particularly sensitive to overexploitation because they are at the northernmost limit of the species' range, living at low densities in areas of relatively low productivity. We could predict, relative to other populations, low reproduction resulting from delayed age at first parturition, longer birth and reproductive intervals, and smaller litter sizes (see, e.g., McLoughlin et al. 2003). Of all polar bear populations, high arctic populations may be most susceptible to impacts of hunting.

We used mark-recapture data collected from 1992 to 1997 to estimate demographic rates and their variances for high arctic polar bears inhabiting Kane Basin, Canada and Greenland (Fig. 1), and harvest risks for the population at estimated size. Polar bears in Kane Basin comprise the most northerly hunted population of bears in North America. Our

demographic analysis included a detailed assessment of age- and sex-specific survival and recruitment from 272 marked polar bears, using information contained within the standing age distribution of captures and survival and abundance estimates from mark-recapture analysis. We incorporated demographic parameters and their variances into a harvest risk analysis designed to consider demographic, process (e.g., environmental), and sampling uncertainty in generating likelihoods of persistence (i.e., a stochastic, harvested Population Viability Analysis [PVA]).

Methods

Species and study area

The natural history, ecology, and life history of polar bears has been described by several authors (Taylor et al. 1987*a,b*; Amstrup and DeMaster 1988; Ramsay and Stirling 1988; Stirling 1988; Amstrup 2000; Ferguson et al. 2000*a,b*). The geographic bounds of the Kane Basin polar bear population (Fig. 1) has also been previously evaluated using movements of marked and recaptured (or harvested) individuals (Taylor and Lee 1995) and movements of radio-collared adult females (Taylor et al. 2001*a*). Our study area in this paper corresponds to the Kane Basin polar bear population identified in Taylor et al. (2001*a*).

Captures, recaptures, and recoveries

From 1992 to 1997, we annually searched the study area by helicopter and captured and marked every bear encountered. We chemically immobilized all bears and their dependent cubs for capture and marking according to procedures described by Stirling et al. (1989), following Animal Care Protocol No. 950005 of the University of Saskatchewan and under guidance of the Canadian Council on Animal Care. Upon initial capture, we assigned an unique identification number to each bear and marked animals accordingly using a plastic ear tag and permanent lip tattoo. We also marked each bear with a wax crayon on the fur to ensure that they were not captured more than once per year. We considered a bear's age as 'known' if the bear was captured as a cub-of-the-year (cub) or yearling, or its age was estimated by counting annular rings of an extracted vestigial premolar (Calvert and Ramsay 1998). The sex, age, family status, and location of all polar bears killed by hunters, killed as problem bears, or found dead from any cause were recorded.

Survival and abundance

Estimates of survival rate and abundance were constructed from capture-recapture data using the Barker model formulation implemented in program MARK (White and Burnham 1999). The Barker likelihood for capture-recapture data is conditioned on initial capture events (i.e., the initial capture is treated as a release). The likelihood is based solely on recapture events of marked (i.e., previously caught) animals, and is defined by user-specified models for survival (S) and (re)capture probabilities (p) that may be expressed as functions of covariates such as sex, age, and time. The Barker model is

essentially three inter-related models: one live-capture model, one harvest-mortality (or recovery) model, and one survival model. However, in our application the harvest mortality did not have to be modeled (i.e., $r = 1$) since it was believed to be entirely known.

We used program MARK to analyze the Kane Basin capture-recapture and harvest data collected from 1992 to 1997. We examined a series of models for capture probability that incorporated potential covariates. We considered a model that allowed capture probability to vary for each year and another model in which capture probability was the same for all years. Within the area searched in a given day, bears were located by visual observation and tracking from a helicopter. Successful location and eventual capture were likely to be affected by the number of bears in a group, their reaction to the helicopter, movement patterns, and fidelity to known areas of high use. Because these factors were also likely to vary for different family classes, we categorized bears into three classes: 1) females, cubs and yearlings; 2) sub-adults (ages 2–4) of both sexes; and 3) adult males, and considered models in which capture probability varied for these classes. We also considered models in which bears with transmitters (radios) had a higher capture probability because their location was known at various times throughout the year. Cubs and yearlings of a female with a transmitter were considered to have the same probability of capture as their mother.

For survival probability, we considered models that included sex, age, and year. More males were harvested than females, but this was captured by including the harvest explicitly. Survival was also likely to vary by age. We expected cubs to have lower survival than non-cubs. We considered an age-specific model which included different survival for cubs, subadults (aged 1–4 years), and adults (5+ years). Annual differences in

environmental conditions could create variation in survival, so we considered models with distinct annual survival rates.

We fitted a series of Barker Cormack-Jolly-Seber (CJS) models using each capture probability model with each survival probability model (White and Burnham 1999). We considered additive models with main effects (e.g., sex + year) but did not consider models with interactions because there were too few data to support the additional complexity. We used Akaike's Information Criterion adjusted for over-dispersion ($QAIC_c$) as a guide for model selection (Burnham and Anderson 1998). The data were likely to be over-dispersed (i.e., greater than binomial variation) because survival and capture events of family groups (e.g., females with cubs or yearlings) were not independent. We estimated the over-dispersion coefficient, $\hat{c}$, based on the number of dependent cub captures relative to all captures (Taylor et al. 2002). We ranked the model with the lowest $QAIC_c$ as best, and we used differences in $QAIC_c$ between the best-fitting model and every other model ($\Delta QAIC_c$) to identify other likely models. We followed Burnham and Anderson (1998) in selecting likely models, where $\Delta QAIC_c < 2.0$, 2.0–4.0, 4.0–7.0, and >7.0 can be said to exhibit strong, some, little, or no support, respectively. We also used program MARK to calculate the $QAIC_c$ weight for each candidate model; these weights sum to 1.0 and represent the relative likelihood of each model (Burnham and Anderson 1998). For models with $\Delta QAIC_c < 4.0$ we used model averaging, weighted according to $QAIC_c$ weights, to present parameter estimates (Burnham and Anderson 1998).

Because the Barker-CJS model likelihood did not include the probability distribution for unmarked animals, it was not likely to have the best precision for estimating abundance when survival and capture probabilities are not time dependent (i.e., constrained

Jolly-Seber model). Thus, although we used the Barker-CJS model formulation to estimate survival rates, we used the Jolly-Seber method to estimate abundance. We used estimated capture probabilities (p) from marked animals in the CJS portion of the Barker-CJS likelihood (Pollock et al. 1990) to estimate abundance (N) for each year i following Taylor et al. (2002). We computed variance estimates for N_i using a Taylor series approximation (Taylor et al. 2002) that contains a component of variance for the number of marks observed and another for estimation of p (Thompson 1992:165).

For cases where we stratified the population into k strata (e.g., sex and age), the total estimated population was the sum of stratum estimates and the variance estimator was extended to include covariances between estimated capture probabilities in the k strata (see Taylor et al. 2002). We used a similar estimator to construct a variance estimate for the average population size over several years.

Our estimates of total survival derived from capture-recapture data, S, included losses from harvest. We were interested in estimating natural survival, S_n, to investigate potential impacts of alternative harvest strategies. Since total harvest of Kane Basin bears was known, we used the approach outlined by Taylor et al. (2002) to estimate natural survival, S_n, from the average annual harvested population size and total survival (S), which assumes that harvest and natural mortality occur in two separate time periods. Here, we also used a Taylor series approximation for the variance of natural survival (Taylor et al. 2002).

Reproduction and population growth rate

We calculated six reproductive parameters for the Kane Basin population based on analysis of the standing age distribution for captures from 1992 to 1997 (Taylor et al. 1987*a* 2000): litter size of cubs, female litter production rates for ages 4, 5, 6, and 7+, and the sex ratio of newborn litters. We calculated the stable-age, zero-harvest population growth rate (δ_N) according to Taylor et al. (1987*b*, 2001*b*) by incorporating the above information on reproduction and survival rates based on mark-recapture analysis.

We used a jack-knife method (Arveson 1969) to obtain variances of life history parameters estimated from the standing age distribution (Taylor et al. 1987*a*, 2000). The data were collected over many years, so our estimates of variance included both sampling error and inter-year variation. Calculations of reproductive parameters were conducted using the Visual Basic program 'Vital Rates' (Taylor et al. 2000). We used Monte Carlo simulations to estimate the mean and standard error (SE) of δ_N using a Visual Basic program called 'RISKMAN' (Taylor et al. 2001*b*). Our estimate of the harvested finite rate of increase, δ_H, was computed in a similar manner by applying the known, average harvest for years 1992–1997 to the population simulation. Both the Vital Rates and RISKMAN programs are available freely from M. K. Taylor upon written request.

Harvest risk analysis

We used RISKMAN, a life-table-based, PVA software program (Taylor et al. 2001*b*, see Taylor et al. 2002; McLoughlin et al. 2003; McLoughlin and Messier 2004) to model risks

of future population declines in this study. Our input for the model included age- and sex-specific schedules of reproduction, survival, harvest, and their variances, as determined through analysis of mark-recapture data, the standing age distribution of captures, and harvest data.

Riskman incorporates stochasticity into its population model at several levels. To incorporate uncertainty in initial population size, simulations can be generated using a random initial population size drawn from a normal distribution with mean and standard error (SE) provided by the user. For each year of simulation, RISKMAN obtains a random normal deviate for each survival and recruitment rate based on an user-specified mean and SE for particular sex and age strata. Individuals in the model are then exposed in a series of Bernoulli trials to the probabilities described by annual random deviates. This process can incorporate annual variability and sampling error, but also uncertainty associated with applying the random mean to individual trials where the result is either a success or a failure (e.g. survival or death, produce a litter or fail to produce a litter). Stochasticity in litter size and sex ratio can also be incorporated into the model. Riskman uses Monte Carlo techniques to generate a distribution of results (Manly 1997), and then uses this distribution to estimate the variance of summary parameters, such as population size at a future time, population growth rate, and proportion of runs that result in a population decline set at a predetermined level by the user. We adopted the latter to estimate persistence probability.

Our approach to variance in this simulation was to pool sampling and environmental variances for survival and reproduction. We did this because: 1) our jack-knife estimator of variances for reproductive parameters did not partition the sampling component of variance from environmental variance, and 2) we were mainly interested in

quantifying the risks of population decline as supported by the data (i.e., from a management, rather than academic, perspective).

For each year of simulation, the frequency of occurrence of unacceptable outcomes (based on our threshold value of a decline >20% of initial population size) was monitored and reported as the cumulative proportion of total runs over the threshold at that time. Individual runs could recover from 'depletion', but not from a condition where all males or all females or both were lost. Required population parameter estimates and standard error inputs included: annual natural survival rate (stratified by age and sex as supported by the data), age of first reproduction, age-specific litter production rates for females available to have cubs (i.e., females with no cubs and females with 2-year-olds), litter size, the sex ratio of cubs, initial population size, and the sex, age, and family status distribution of the harvest.

We ran harvest simulations for 15 years using natural survival rates, upon which harvest was added (0–11 bears/year). Simulations were time referenced to 1997 which was the last year of sampling. We selected 15 years as a simulation interval because we estimated that the fraction of the Kane Basin population that would still be marked after 15 years (i.e., ~10%) would be sufficient to re-estimate the population at the next population inventory.

Results

Captures, recaptures, and recoveries

We captured 272 individual polar bears in the study area from 1992–1997 (Table 1). Of 84 female bears caught within the period of study, 24 bears were recaptured at least once during 1993–1997 with a total of 40 recaptures, of which 10 were radio-collared bears. Of 47 male bears caught between 1992–1997, 17 bears were recaptured at least once during 1993–1997, with a total of 24 bear recaptures. The harvest between 1992 and 1997 was highly selective for male bears and averaged 10.6 bears/year, SE = 0.5 (PBTC 2001).

Survival and abundance

Our best-fitting model specified age effects in probabilities of survival/recovery and an effect of possessing a radio transmitter on capture probability (Table 2). Three additional models were sufficiently close to the best-fitting model to be included in a model average (Table 2): a model identical to the above that added a sex effect to survival/recovery probability, and models identical to the top two that included effects of family group associations on capture probability. Model averaged, annual mean total survival rates (S) and mean natural survival rates (S_n) are presented in Table 3.

Annual estimates of total abundance (1994–1997) averaged 164 bears (SE = 34.6), of which 97 (SE = 21.3) were female and 67 (SE = 15.6) were male. Of these, 34 bears

were cubs (SE = 8.7) and 54 bears (SE = 12.2) were adult females, suggesting an average

natality (cubs per adult female) of 0.63.

Reproduction and population growth rate

Summary reproductive parameters for the Kane Basin population based on analysis of the

standing age distribution for captures from 1992–1997 included means for litter size of

cubs (1.667, SE = 0.083), female litter production rates for ages 4 (0.000, SE = 0.000), 5

(0.000, SE = 0.000), 6 (0.357, SE = 0.731), and 7+ (0.978, SE = 0.085), and the sex ratio of

newborn litters (0.426 male, SE = 0.029). We calculated the stable-age, zero-harvest

population growth rate, δ_N, as 1.009 (SE = 0.007). The harvested population growth rate,

δ_H, was 0.922 (SE = 0.015).

Harvest risk analysis

Our results suggest the current harvest of Kane Basin polar bears is unsustainable. For the

immediate future (i.e., next 15 years), the population can be expected to decline if harvest

remains at present levels without replenishment from immigration (Fig. 2). Since the

estimated unharvested population growth rate for Kane Basin polar bears ($\delta_N = 1.009$)

determines the time required for recovery from present levels, even if left unharvested

recovery of the population to abundance levels >200 bears will likely take long periods of

time (e.g., 20+ years).

Discussion

In extreme environments, female mammals should allocate resources for reproduction in a safer but less-productive manner (Ferguson and McLoughlin 2000). Changes in life history that affect timing of reproduction (e.g., later age at maturity, longer interbirth intervals, greater longevity; Cohen 1970; Phillipi and Seger 1989; Sajah and Perrin 1990) reduces effects of extreme or stochastic environments, such that the geometric mean fitness of individuals is increased (Yoshimura and Jansen 1996). Polar bears in Kane Basin exhibit life history traits that appear adapted to extremes of the species' fundamental niche, including late reproduction relative to other polar bear populations (e.g., no litter production until age six) and high natural annual adult survival (e.g., 0.997, versus adult female survival ranging from 0.946 to 0.977 for six more southerly populations of polar bears in Nunavut; PBTC 2001; Taylor et al. 2002, 2004). We did not, however, detect any difference between the litter size of Kane Basin polar bears and other polar bear populations. Similar reaction norms in life history have been observed for grizzly bear populations in response to changes in productivity and seasonality of the environment, including insensitivity of litter size to changes in habitat quality (Ferguson and McLoughlin 2000).

For large mammals, the end result of life history adaptations to extreme environments is relatively low natural (unharvested) rates of population increase when populations are below carrying capacity. The unharvested finite rate of increase observed for polar bears inhabiting Kane Basin is an example ($\delta_N = 1.009$), barely exceeding unity

even after what we suspect has been a prolonged period of overharvest (i.e., the population is clearly not at carrying capacity). This rate contrasts significantly with unharvested population growth rates obtained for adjacent populations of polar bears, including the Baffin Bay population to the immediate south ($\mathscr{S}_N = 1.051$; Taylor et al. 2004). Intraspecific variation in life history entails that not all populations of a species can, or should, be harvested at the same rates. Populations with relatively low intrinsic (Malthusian) rates of increase may not be safely harvested at levels that appear to be sustainable for conspecific populations (McLoughlin et al. 2004). We caution against applying harvest rates to polar bears within Kane Basin that were originally developed from data on polar bears from outside the Kane Basin boundary.

Although the difference between the annual harvest rate and unharvested growth rate of a population plays the primary role in determining sustainability of a given harvest, it is not the only consideration when we estimate likelihoods of population persistence. If populations are small, population size requires special consideration when developing hunting quotas that allow for acceptable probabilities of population persistence. Discrete demographic units that are small in size are more susceptible to population decline due to the phenomenon of increasing importance of random chance in survival and reproduction in determining population trends as population size decreases (i.e., demographic stochasticity; Caughley 1977). Deterministic Allee effects (Allee 1931; Boyce 1992) may also contribute to 'extinction thresholds' for small populations, whereby individuals of populations that have been significantly reduced have difficulty finding mates, or are unable to engage in normal social interactions, resulting in per capita growth rates that approach or fall below zero at lower densities. The Kane Basin population is relatively small ($N = 164$), with an

estimate of only 54 adult females. Several authors have cautioned against hunting discrete

demographic units approaching 100 individuals due to unknown and potentially severe

Allee effects or effects of demographic stochasticity (e.g., for bears, Wielgus 2002;

McLoughlin et al. 2004).

Although we predict a continued decline of the Kane Basin population of polar

bears—if the average harvest rate is not decreased from present levels—it is possible

through emigration from the nearby, and much larger ($N > 2000$; Taylor et al. 2004), Baffin

Bay population that polar bears may continue to be harvested in Kane Basin without any

observable decrease in population size. What is key here is the degree to which individuals

within Kane Basin constitute a discrete demographic unit. Although cluster analysis of

movement data suggests this to be the case (Taylor et al. 2001*a*), genetic evidence suggests

that the Baffin Bay and Kane Basin populations have not been isolated genetically (Paetkau

et al. 1999).

Our risk assessment is an expression of the uncertainty in demographic processes

and parameters. Our simulations suggest that a quota of <2 bears may be reasonable for

this population, if the management goal also includes recovery to prior levels of abundance.

Higher harvest rates constitute an increased risk (fewer acceptable outcomes) to the

population, and will result in slower recovery rates. If managers and stakeholders are

willing to accept a very long recovery time, or a large degree of risk associated with the

recovery, harvesting is possible; however, the shortest recovery time and smallest risk

obviously comes from instituting a harvest moratorium.

Even when risk has been quantified, periodic monitoring is still required if the

harvest level poses a significant risk to populations. Small populations limit the possible

sample size of demographic studies and increase the uncertainty of estimates and demographic projections. Thus, the more a population is reduced, the more conservative the management response should be. To ensure a timely recovery, total anthropogenic mortality from all sources (i.e., harvest, defense, accidental, and illegal) must be reduced to levels that pose essentially no risk to the population, or the recovery must be monitored to ensure that the population is not further compromised. Inuit hunters depend on polar bears for social and cultural needs as well as for food and to support the traditional economy. These needs must also be considered when formulating a recovery strategy. Whatever harvest level is chosen, stakeholders should be informed that quota recommendations are based on uncertain information and that long-term harvest moratoriums may be required to regain population size.

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Table 1 Initial captures of polar bears of Kane Basin, Canada and Greenland, 1992–1997. In parentheses, the number of bears recaptured at least once in the years 1993–1997 is listed, followed by the number of bears recovered in the harvest during the harvest years 1993–1997. Bears initially caught in 1997 have no chance of recapture, which is indicated by an asterisk.

Sex	Year	Cub	Yearling	2-yr old	3-4 yr old	5 to 20 yr	>20 yr	Total
Female	1992	4 (0,0)	0 (0,0)	0 (0,0)	2 (1,1)	5 (2,0)	0 (0,0)	11 (3,1)
	1993	1 (0,0)	2 (1,0)	1 (0,0)	0 (0,0)	6 (5,0)	0 (0,0)	10 (6,0)
	1994	4 (0,2)	0 (0,0)	0 (0,0)	3 (2,0)	7 (6,0)	0 (0,0)	14 (8,2)
	1995	12 (2,1)	0 (0,0)	2 (0,0)	4 (1,2)	13 (2,3)	0 (0,0)	31 (5,6)
	1996	4 (0,0)	1 (1,0)	1 (0,0)	1 (0,0)	6 (1,0)	0 (0,0)	13 (2,0)
	1997	0 (*,0)	3 (*,0)	1 (*,0)	1 (*,0)	0 (*,0)	0 (*,0)	5 (0,0)
Total		25(2,3)	6(2,0)	5(0,0)	11(4,3)	37(16,3)	0(0,0)	84(24,9)
Male	1992	1 (0,0)	0 (0,0)	0 (0,0)	0 (0,0)	3 (2,0)	0 (0,0)	4 (2,0)
	1993	3 (2,0)	1 (0,0)	0 (0,0)	0 (0,0)	7 (4,2)	1 (1,0)	12 (7,2)
	1994	4 (1,1)	0 (0,0)	0 (0,0)	2 (0,1)	2 (2,0)	0 (0,0)	8 (3,2)
	1995	5 (0,0)	3 (0,0)	0 (0,0)	5 (0,0)	5 (3,3)	1 (0,0)	19 (3,3)
	1996	2 (0,0)	1 (0,0)	0 (0,0)	2 (1,0)	2 (1,0)	0 (0,0)	7 (2,0)
	1997	3 (*,0)	1 (*,0)	0 (*,0)	0 (*,0)	3 (*,0)	0 (*,0)	7 (0,0)
Total		18(3,1)	6(0,0)	0(0,0)	9(1,1)	22(12,5)	2(1,0)	47(17,7)

Table 2)QAIC$_c$ values for models fitted to Kane Basin capture-recapture and harvest recovery data, 1992–1997. The number of estimated parameters for each sub-model is shown in parentheses. Bolded values represent models used in model averaging. Our estimate of the overdisperson coefficient, $\hat{c}$, was ___. QAIC$_c$ weights of the best four models, ranked from highest to lowest, were 0.397, 0.323, 0.159, and 0.121, respectively.

Survival/Recovery Model	Capture Probability Model		
	Radio (1)	Radio + Year (4)	Radio + Age/Sex (2)
Constant (2)	10.47	17.07	4.69
Sex (4)	14.50	21.26	8.74
Age (6)	**0**	4.88	**1.83**
Age + Sex (8)	**0.41**	7.75	**2.38**

Table 3 Means and standard errors (SE) of natural (no harvest,) survival and actual (includes harvest) survival rates for the Kane Basin polar bear population, 1992–1997. Estimates are given for the weighted-averaged four best Barker MARK models.

Sex and Age	Mean Annual Survival Rate (SE)	
	No Harvest	Harvest
Female		
0	0.410 (0.200)	0.374 (0.180)
1–4	0.756 (0.159)	0.686 (0.157)
5+	0.997 (0.026)	0.967 (0.043)
Male		
0	0.345 (0.200)	0.308 (0.172)
1–4	0.663 (0.197)	0.617 (0.180)
5+	0.997 (0.026)	0.957 (0.046)

Figure Captions

Fig. 1 Location of the Kane Basin (KB) polar bear population, Canada and Greenland, 1992–1997. Boundaries are defined as in Taylor et al. (2002).

Fig. 2 Estimated likelihood of >20% decline from initial population size (i.e., 164 bears) vs. annual harvest rate (bears/year) for polar bears inhabiting Kane Basin, Nunavut, after 15 years. The star indicates the mean annual harvest rate for the period of study (1992–1997).
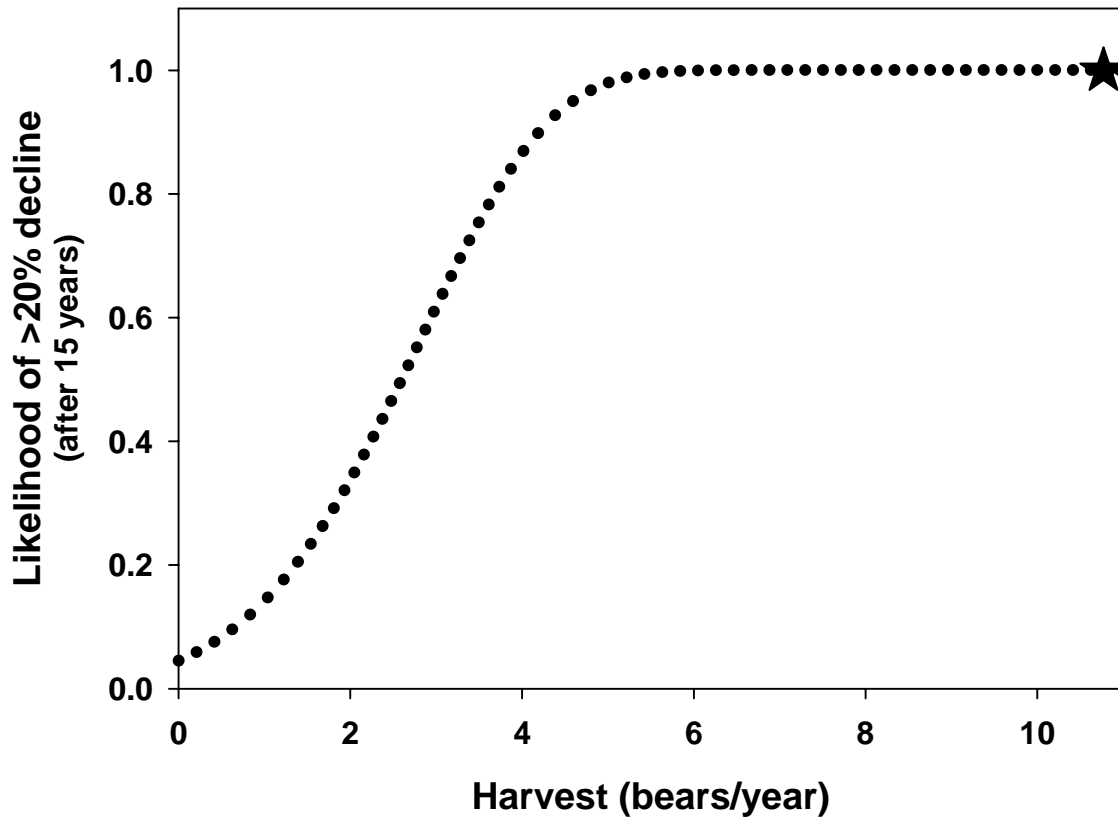
Fig. 1.

Fig. 2