Modelling the mating system of polar bears: a mechanistic approach to the Allee effect

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Allee effects may render exploited animal populations extinction prone, but empirical data are often lacking to describe the circumstances leading to an Allee effect. Arbitrary assumptions regarding Allee effects could lead to erroneous management decisions so that predictive modelling approaches are needed that identify the circumstances leading to an Allee effect before such a scenario occurs. We present a predictive approach of Allee effects for polar bears where low population densities, an unpredictable habitat and harvest-depleted male populations result in infrequent mating encounters. We develop a mechanistic model for the polar bear mating system that predicts the proportion of fertilized females at the end of the mating season given population density and operational sex ratio. The model is parametrized using pairing data from Lancaster Sound, Canada, and describes the observed pairing dynamics well. Female mating success is shown to be a nonlinear function of the operational sex ratio, so that a sudden and rapid reproductive collapse could occur if males are severely depleted. The operational sex ratio where an Allee effect is expected is dependent on population density. We focus on the prediction of Allee effects in polar bears but our approach is also applicable to other species.

Keywords: component Allee effect; two-sex model; *Ursus maritimus*; sex-selective harvest; population density; operational sex ratio

1. INTRODUCTION

Much attention has been devoted to the study of Allee effects in recent years, a phenomenon where individuals benefit from the presence of conspecifics and suffer from a decrease in some component of fitness at low population sizes or densities (Fowler & Baker 1991; Sæther *et al.* 1996; Stephens *et al.* 1999; Boukal & Berec 2002). While many mechanisms could give rise to an Allee effect (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Berec *et al.* 2007), by far the most commonly studied is the difficulty of finding mates at low population densities (e.g. Dennis 1989; McCarthy 1997; South & Kenward 2001; Boukal & Berec 2002). Decreased probabilities of finding a mate at low densities result in decreased reproductive success, and thus a positive relationship between this component of fitness and population density.

The harvest of animal populations can have unforeseen consequences if Allee effects are not recognized (Courchamp *et al.* 1999; Stephens & Sutherland 1999). Allee effects can accelerate population decline, possibly even leading to extinction. Recently, Allee effects, initiated by inappropriate harvesting, have been demonstrated for saiga antelopes (*Saiga tatarica*; Milner-Gulland *et al.*

2003), African wild dogs (*Lycaon pictus*; Courchamp & Macdonald 2001), African elephants (*Loxodonta africana*; Poole 1989) and moose (*Alces alces*; Solberg *et al.* 2002). An Allee effect has also been proposed for the slow recovery and continuing declines in Atlantic cod (*Gadus morhua*; Rowe *et al.* 2004), and possibly other commercially exploited fish stocks (Liermann & Hilborn 1997). Even the extinction of the passenger pigeon (*Ectopistes migratorius*) involved harvesting and was possibly accelerated by an Allee effect (Halliday 1980).

The potential impact of Allee effects on population persistence makes it crucial to determine the circumstances leading to an Allee effect before such a scenario is reached. Such knowledge would aid the implementation of optimal harvesting strategies or the direction of conservation efforts, particularly for threatened and endangered species existing at low population sizes or densities, but not yet showing an Allee effect, such as North Atlantic right whales (*Eubalaena glacialis*; Fujiwara & Caswell 2001), Amur tigers (*Panthera tigris*; Carroll & Miquelle 2006) or polar bears (*Ursus maritimus*). Unlike smaller organisms where Allee effects can sometimes be demonstrated in laboratory populations (e.g. Allee 1931), empirical data on Allee effects cannot be gathered for large free-ranging species before an Allee effect occurs. Thus, predictive methods are needed.

In this paper, we present such a predictive approach for polar bears. These solitary, non-territorial animals occur

at low densities and are vulnerable to Allee effects due to low frequencies of potential mating encounters. The unpredictability of the Arctic sea ice, and the consequent unpredictability of the spatial distribution of mates, makes mate-searching an important variable in their reproductive dynamics (Ramsay & Stirling 1986).

A male-biased operational sex ratio with two to three males for every available female results from a prolonged mother–offspring bond, and ensures high female mating success in unharvested populations (Ramsay & Stirling 1986). However, prolonged sex-selective harvest has significantly reduced the numbers of adult males in all Canadian polar bear populations, leading to balanced or even female-biased operational sex ratios (Lee & Taylor 1994; Derocher *et al.* 1997). Nonetheless, management policies encourage hunters to select for males so that at least two-thirds of the harvest is male (Freeman & Wenzel 2006; Taylor *et al.* in press a). This selective removal of males, and the generally higher vulnerability of males to harvest (Lee & Taylor 1994), has led to concerns that male populations could be depleted to a point where many females become unable to find mates (Derocher *et al.* 1997; McLoughlin *et al.* 2005).

Mating season length and the time allocated to mate-searching and mating limit the number of females each male can locate and fertilize. Consequently, there will be a sex ratio below which female fertilization rates decline due to male scarcity (Caughley 1977). Determining this sex ratio, and thus understanding how many males are needed to maintain stable populations, is therefore crucial for the evaluation of current and future harvesting strategies. However, no Allee effect has yet been reported for polar bears and fertilization rates are not directly monitored. Thus, no empirical data exist on the relationship between fertilization rates and male and female densities, and a modelling approach is needed.

One-sex models can sometimes be used to detect Allee effects in cases where appropriate data exist (Myers *et al.* 1995; Morris 2002). However, they have low predictive power for Allee effects arising from a difficulty of finding mates and cannot be used to validate management strategies *a priori* (Boukal & Berec 2002) because an individual's success in finding a potential mate is not only influenced by population density, but also by population sex ratio (Legendre *et al.* 1999; Bessa-Gomes *et al.* 2004; Rankin & Kokko 2007). Two-sex models are more appropriate because they explicitly address mate shortage. In fact, models that aim to understand the effects of a depleted male population should explicitly consider the mating system (Legendre *et al.* 1999; Engen *et al.* 2003; Bessa-Gomes *et al.* 2004; McLoughlin *et al.* 2005) and accurately fit historical data (Stephens *et al.* 2002; Haefner 2005), particularly when the objective is the prediction of Allee effects (Boukal & Berec 2002). Although two-sex models have been studied, investigations were mostly theoretical (e.g. Caswell & Weeks 1986; Lindström & Kokko 1998; Ranta *et al.* 1999; Bessa-Gomes *et al.* 2004; Rankin & Kokko 2007); the application of two-sex models to biological data remains scarce (but see Stephens *et al.* 2002; Hurford *et al.* 2006).

Recent work highlights the importance to distinguish between a *component* Allee effect, defined as a positive relationship between any component of individual fitness and population density or number, and a *demographic* Allee effect, which is a positive relationship between the *per capita* growth rate and population density or number (Stephens *et al.* 1999). Decreased success in finding mates due to low densities or skewed sex ratios should be considered a component Allee effect, which may or may not translate into a demographic Allee effect (Stephens *et al.* 1999). As a first step in understanding the effects of sex-selective polar bear harvest, our objective is to predict fertilization rates from male and female densities, and thus identify circumstances leading to such a component Allee effect.

For this purpose, we develop a mechanistic model for the mating system of polar bears: we extend the dynamical systems framework of Wells *et al.* (1990) and Veit & Lewis (1996) to track solitary males, solitary females and breeding pairs through the mating season, including pair formation and separation explicitly. A possible component Allee effect arises naturally through the proportion of females that have not mated by the end of the mating season. Using a maximum likelihood approach, we estimate model parameters by fitting the predicted pairing dynamics to observed pairing data from the population of Lancaster Sound, Canada. Model inputs are the densities of sexually active males and females; model output is the proportion of females fertilized by the end of the mating season. This simple, biologically realistic; model can be used to specify the conditions leading to a component Allee effect of reduced fertilization rates due to a lack of males.

We begin by introducing the study population, and then proceed to development, parametrization and analysis of the mating model.

2. STUDY AREA, DATA COLLECTION AND DEFINITIONS

We used data collected during the most recent polar bear population inventory of Lancaster Sound, Nunavut, Canada. Each year from 1993 to 1997, the population area was systematically searched from early April to early June in a geographically uniform manner, with every bear seen captured. For each bear, we recorded age, sex, reproductive status and pairing status. The sampling season varied slightly between years, with the earliest sampling on 3 April, the latest on 6 June.

Ages were determined for older bears by counting the annular rings of an extracted vestigial premolar tooth (Calvert & Ramsay 1998) and for younger bears (up to 1 year) by tooth eruption patterns. We defined males as sexually mature if they were at least 5 years old. Although intense competition for females might prevent young males from mating (Ramsay & Stirling 1986), most 5-year-olds are physically mature (in contrast to the majority of 4-year-olds) and would be capable of breeding if an opportunity arose (Rosing-Asvid *et al.* 2002). Females were regarded as sexually mature if they were at least 4 years old because 5-year-old females can produce cubs after mating the year before (Furnell & Schweinsburg 1984). Immature bears and females accompanied by cubs-of-the-year or yearlings were considered unavailable for mating (Ramsay & Stirling 1986) and excluded from further analyses. Because most cubs are weaned at 2.5 years of age in the high Arctic, and females can come into oestrus that same season (Lentfer *et al.* 1980; Ramsay & Stirling 1986), we treated females with 2-year-olds as available-to-breed and pooled them with females without cubs.

We further classified bears as solitary or paired. A bear was paired if captured with a mature bear of the opposite sex and behaving in a manner that suggested pairing. In instances where several males were associated with a female (10.9% of breeding pairs), we considered the oldest attending male as paired and the other males as solitary. A few individuals were captured twice (2.9% of males and 2.1% of females) during the same season. Second captures were included in our pairing dynamics analyses, because a bear can change between being solitary and paired throughout the mating season.

3. MODEL DEVELOPMENT

(a) *The mating system of polar bears*

Males locate females by following their tracks. Subsequently formed breeding pairs last between one and four weeks (Ramsay & Stirling 1986; Wiig *et al.* 1992). Males are thought to be polygynous (Berta & Sumich 1999), locating, defending and fertilizing females one after another. The number of females a male can locate during a mating season is unknown, but probably depends on mating season length, the time for mate location and the length of pair associations. Furthermore, the ability of males to continue mate-searching after pairs separate may play a role. Mate-searching is demanding, and males often forego feeding during the mating season, focusing on reproduction instead. Younger males, still growing, may be limited in their searching ability by their need to forage.

Ramsay & Stirling (1986) and Wiig *et al.* (1992) suggested that polyandry might occur with females consecutively forming breeding pairs with different males, but the frequency of such events is unknown. However, the maximum time a female will associate with males is restricted by the oestrus period, which can last up to four weeks (Wiig *et al.* 1992).

Mating season length and timing are unclear. Breeding pairs were reported as early as March (Lønø 1970; Lentfer *et al.* 1980), and Rosing-Asvid *et al.* (2002) suggested a mating season extended from early March to early June, with a peak between April and early May. The levels of serum steroid concentrations in male polar bears, however, suggest a mating season from early April to late May (Palmer *et al.* 1988; Howell-Skalla *et al.* 2002).

(b) *Model assumptions and structure*

We model the pairing dynamics of a polar bear population during the mating season using five differential equations and explicitly incorporate pair formation, pair separation and the ability of males to continue mate-searching after pair separation. We consider only mature males and mature females not accompanied by cubs-of-the-year or yearlings. Females with 2-year-old cubs are considered as available-to-breed, and we do not distinguish between them and females without young in the following:

$$\underbrace{\frac{\mathrm{d}M}{\mathrm{d}t}}_{\substack{\text{solitary}\\\text{available males}}} = -\underbrace{\sigma MF}_{\text{pair formation}} + \underbrace{\alpha\mu P}_{\substack{\text{males available}\\\text{after pair separation}}}, \quad (3.1a)$$

$$\underbrace{\frac{\mathrm{d}F}{\mathrm{d}t}}_{\text{unfertilized females}} = -\underbrace{\sigma MF}_{\text{pair formation}}, \quad (3.1b)$$

$$\underbrace{\frac{\mathrm{d}P}{\mathrm{d}t}}_{\text{breeding pairs}} = \underbrace{\sigma MF}_{\text{pair formation}} - \underbrace{\mu P}_{\text{pair separation}}, \quad (3.1c)$$

$$\underbrace{\frac{\mathrm{d}M^*}{\mathrm{d}t}}_{\text{solitary unavailable males}} = \underbrace{(1-\alpha)\mu P}_{\substack{\text{males unavailable}\\\text{after pair separation}}}, \quad (3.1d)$$

$$\underbrace{\frac{\mathrm{d}F^*}{\mathrm{d}t}}_{\text{ferilized females}} = \underbrace{\mu P}_{\text{pair separation}}, \quad (3.1e)$$

where $M(t)$, $M^*(t)$, $P(t)$, $F(t)$ and $F^*(t)$ represent the respective densities (at time t) of solitary males searching for mates, solitary males that have ceased searching for mates, breeding pairs, solitary unmated females and solitary mated females now fertilized that have become unavailable for mating, respectively. We assume that all mated females are fertilized.

Adult males and adult females without cubs-of-the-year or yearlings show similar habitat preferences (Stirling *et al.* 1993). We therefore assume them to be randomly distributed in space within the population boundaries and well mixed, and model the process of pair formation using the law of mass action, which gives rise to a nonlinear interaction term. The parameter σ represents hereby the rate of pair formation. Pairs are assumed to remain together for $1/\mu$ time units, so that pairs dissolve at rate μ. To account for variability in the ability of males to focus on mate-searching rather than foraging, we assume that after pair separation males become unavailable with probability $1-\alpha$ to fertilize other females. $\alpha=1$ implies that all solitary males search for mates at all times and $\alpha=0$ represents the limiting case of male monogamy. The parameter α is termed male mating ability.

We do not model polyandry explicitly, although some females may subsequently associate with different males within a period constrained by oestrus. Such behaviour would reduce the number of solitary males for prolonged periods and could affect population mating success by lowering the chances of other females to mate. However, if mate-searching between consecutive pairings is negligibly short, then polyandry is sufficiently represented through prolonged pair associations, and, thus, the parameter μ.

We assume that all mature males and all mature females that are not accompanied by cubs-of-the-year or yearlings are solitary and available for breeding at the beginning of the mating season:

$$M(0) = m_0 \qquad (3.2a)$$

$$F(0) = f_0 \qquad (3.2b)$$

$$P(0) = M^*(0) = F^*(0) = 0, \qquad (3.2c)$$

where m_0 denotes the density of mature males and f_0 denotes the density of mature females not accompanied by cubs-of-the-year or yearlings. We assume that m_0 and f_0 remain constant throughout the mating season, as implied by (3.1a)–(3.1e) and (3.2a)–(3.2c):

$$M(t) + P(t) + M^*(t) = m_0 \qquad (3.3a)$$

$$F(t) + P(t) + F^*(t) = f_0. \qquad (3.3b)$$

The mating season starts at $t=0$ and lasts T time units. Female mating success is defined as the proportion of females fertilized by the end of the mating season and is

Table 1. Population size and model parameters for the Lancaster Sound polar bear population. (The brackets next to the maximum likelihood estimates for σ and $1/\mu$ show the bootstrapped 95% CIs. For details regarding the methods of estimation, see main text.)

parameter	definition	estimate	units	method of estimation
population size estimates				
—	no. of mature males	489	bears	mark–recapture
—	no. of mature females not accompanied by cubs-of-the-year or yearlings	451	bears	mark–recapture
—	habitat area	238 862	km^2	total marine area within population boundaries
model parameter estimates				
m_0	density of males available for mating at the beginning of the mating season	2.05	bears per 1000 km^2	no. of mature males/habitat area
f_0	density of females available for mating at the beginning of the mating season	1.89	bears per 1000 km^2	no. of mature females not accompanied by cubs-of-the-year or yearlings/habitat area
m_0/f_0	operational sex ratio	1.08	—	—
σ	pair formation rate	2.05 (1.27; 3.42)	km^2 h^{-1}	maximum likelihood
$1/\mu$	length of pair association	17.5 (14.1; 21.6)	days	maximum likelihood
α	male mating ability	1	—	fixed for parameter estimation and simulations to estimate female mating success (assumption of maximal mating ability)
t_0	first day of the mating season	2 Apr	—	one day before the first day of sampling
T	mating season length	60	days	fixed to estimate female mating success

given by $1 - F(T)/f_0$. We therefore assume all mated females to be fertilized, including females that may still be paired at the end of the mating season.

We explored a range of additional models to accommodate uncertainties in mate-searching behaviour, including a model with a rest stage for polygynous males after mating and a model that explicitly included another period of mate-searching between consecutive pairings for polyandrous females. Because these more complex models were not supported significantly better by the data, we use the simple model (3.1*a*)–(3.1*e*) throughout.

(c) *Parameter estimation*
The densities of available males and females at the beginning of the mating season were estimated as

m_0 = no. of mature males/habitat area,

f_0 = no. of mature females not accompanied by cubs-of-the-year or yearlings/habitat area.

The respective male and female numbers were estimated using sex-specific population size estimates (Taylor *et al.* in press *b*) and the standing age and reproductive stage structure in captures, which were assumed to be representative of the population (table 1). Habitat area was estimated as the total marine area within population boundaries using a geographical information system (ArcGIS 9.1, Environmental Systems Research Institute, Redlands, California, USA). The geographical population boundaries were previously established using mark–recapture movement data (Taylor & Lee 1995), DNA analysis (Paetkau *et al.* 1999) and cluster analysis of radio-telemetry data (Bethke *et al.* 1996; Taylor *et al.* 2001). The ratio m_0/f_0 will henceforth be referred to as the operational sex ratio.

The parameters σ and μ were estimated using maximum likelihood, fitting the predicted to the observed

pairing dynamics. The maximum likelihood function was adapted to our sampling design and is based on the respective proportions of males, females and pairs in each sample. The derivation is presented in appendix A. We pooled the pairing data by day-of-the-year for the purpose of parameter estimation, assuming that mating season timing and associated pairing dynamics do not differ between years; annual variation is unlikely because photoperiod probably regulates the reproductive cycle of polar bears (Palmer *et al.* 1988). For simplicity, we fixed 2 April as the start of the mating season, t_0, assuming that all females come into oestrus that day. Although this is consistent with the estimates of early April as the start (Palmer *et al.* 1988), an earlier beginning of the mating season is possible (Rosing-Asvid *et al.* 2002). We explored the sensitivity of model parameter estimates and mating success predictions to this simplifying assumption by allowing pair formations before 2 April and estimating an additional free parameter, the density of pairs already formed on 2 April, $P(0) = p_0$, through maximum likelihood. However, because this only slightly changed the maximum likelihood estimates for σ and μ (by less than 5% and less than 3%, respectively), mating success predictions were not affected significantly, so that the simplifying assumption regarding t_0 seems appropriate. It is not necessary to fix mating season length for the estimation of σ and μ. However, we set $T = 60$ days to estimate female mating success, $1 - F(T)/f_0$, corresponding to an end of the mating season on 31 May (Howell-Skalla *et al.* 2002; Rosing-Asvid *et al.* 2002).

As the pairing dynamics were insensitive to α, we were unable to estimate this parameter from data. Instead, we fixed $\alpha = 1$ for model fitting, assuming maximal male mating ability, because older males dominate the pairing dynamics in this high-density population. This assumption did not significantly affect the maximum likelihood

estimates of σ and μ. However, reduced male mating abilities could negatively affect female mating success under different initial conditions, such as female-biased operational sex ratios. This is explored in §4.

4. RESULTS AND MODEL ANALYSIS

Of the 261 mature males and 220 mature available females sampled, 64 males and females were paired (24.5 and 29.1%, respectively). Breeding pairs were observed between 5 April and 28 May. Pairing activity peaked around mid-April followed by a slow decline in the proportions of paired males and females until the end of May (figure 1). In April, 33.8% of sampled males and 40.7% of sampled females were paired, in contrast to May, when only 15.3% of males and 17.9% of females were paired.

The model captures these pairing dynamics well. After early pair formations, a broad peak in the proportions of paired males and females is predicted due to prolonged pair associations. A gradual decline in the proportion of breeding pairs follows as pairs separate and fewer unfertilized females are available for pairing (figure 2). Pair formation rate was estimated as $\sigma = 2.05 \, \mathrm{km^2 \, h^{-1}}$ (bootstrapped 95% CI: 1.27–$3.42 \, \mathrm{km^2 \, h^{-1}}$), length of pair association as $1/\mu = 17.5$ days (bootstrapped 95% CI: 14.1–21.6 days; table 1). Opportunistic field observations of pair association lengths range from at least 7 to at least 22 days (Ramsay & Stirling 1986; Wiig *et al.* 1992), giving us additional confidence in our parameter estimate.

Using these parameter estimates, the model predicts female mating success from male and female densities, m_0 and f_0, male mating ability, α, and mating season length, T. Figure 3 summarizes these predictions with contour lines giving mating success as a function of male and female densities, assuming maximal male mating ability ($\alpha = 1$) and $T = 60$ days as mating season length. No component Allee effect due to male scarcity was predicted for the Lancaster Sound population, with 99% of females fertilized by 31 May (bootstrapped 95% CI: 94.5–100.0%; figure 3). This estimate closely corresponds to the observed litter production rate of 95.4% for older adult females (age ≥ 7 years) in Lancaster Sound (Taylor *et al.* in press *b*), i.e. for females where litter production rates are least affected by failed pregnancies.

However, mating success is a strongly nonlinear function of the operational sex ratio m_0/f_0. Therefore, once mating success starts declining due to male scarcity, a small additional loss of males will result in a strong reduction in mating success, suggesting a rapid reproductive collapse. Figure 4 illustrates this relationship for five representative densities (IUCN 2006), varying the operational sex ratio, but keeping the overall density of breeding males and females, $m_0 + f_0$, constant.

Furthermore, mating success depends not only on the operational sex ratio, but also on the overall density of available breeders, $m_0 + f_0$ (figure 4a). As density decreases, an increasing proportion of males is required to maintain a constant level of mating success. For example, while $m_0/f_0 = 0.67$ is sufficient to achieve 95% mating success at the estimated density of available breeders in Lancaster Sound, $m_0/f_0 = 1.55$ is needed at half that density and $m_0/f_0 = 4.43$ at one-third that density. Moreover, 95% mating success cannot be achieved with realistic operational sex ratios at one-quarter that density
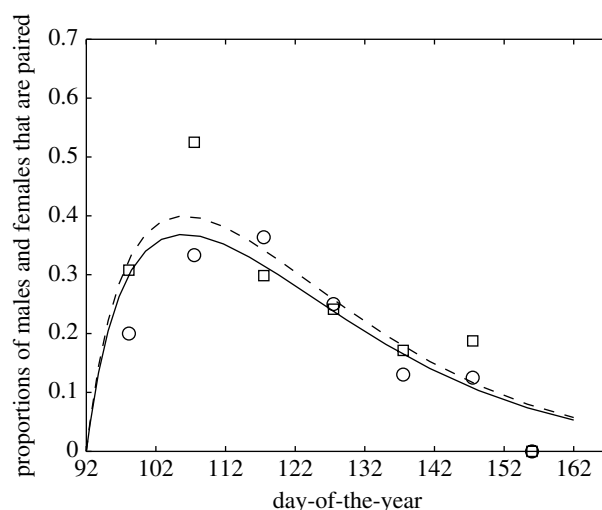
Figure 1. Observed and predicted proportions of mature males (observed, circles; predicted, solid line) and mature females not accompanied by cubs-of-the-year or yearlings (observed, squares; predicted, dashed line) paired on a given day during the mating season in Lancaster Sound. Data are pooled by day-of-the-year across the study period (1993–1997), and (for illustrative purposes only) over 10-day intervals, starting on the first sampling day. Initial conditions for the pairing dynamics simulation were 489 mature males and 451 mature females not accompanied by cubs-of-the-year or yearlings. Parameters were estimated using maximum likelihood ($\sigma = 2.05 \, \mathrm{km^2 \, h^{-1}}$, $\mu = (17.5 \, \mathrm{days})^{-1}$), assuming maximal male mating ability ($\alpha = 1$), and using $t_0 = 2$ April as the first day of the mating season.
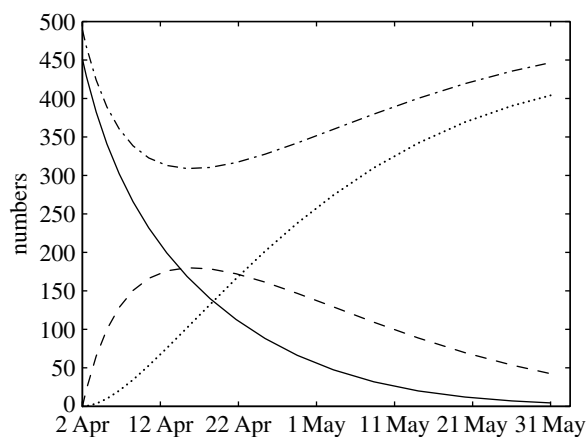

Figure 2. Simulated pairing dynamics during the mating season in Lancaster Sound, showing the predicted numbers of solitary males (dot-dashed line), breeding pairs (dashed line), solitary unfertilized (solid line) and solitary fertilized females (dotted line) as a function of time.

(figure 4a). The latter two examples illustrate the possibility of a component Allee effect of reduced female mating success at low densities even at the natural operational sex ratio of two to three males per available female. However, although relatively fewer males are required to maintain mating success at higher densities, a potential reproductive collapse resulting from male scarcity would also be faster and more sudden at higher densities owing to the increasing nonlinearity between mating success and the operational sex ratio (figure 4a).

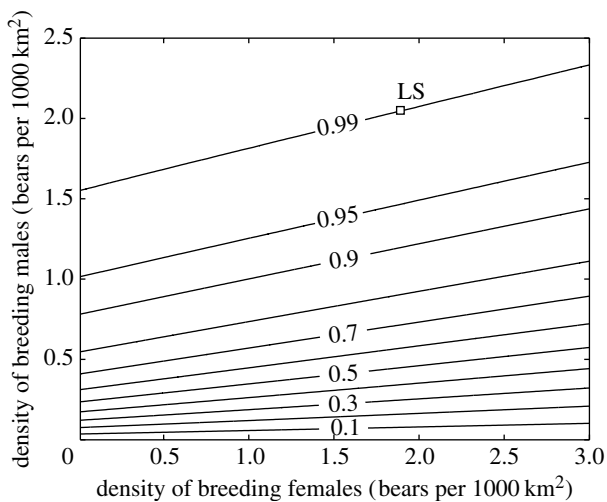The nonlinear relationship between female mating success and the operational sex ratio arises regardless of

Figure 3. Contour lines giving female mating success as a function of male and female densities, using the maximum likelihood parameter estimates from Lancaster Sound ($\sigma = 2.05$ km^2 h^{-1}, $\mu = (17.5$ days$)^{-1}$) and assuming maximal male mating ability ($\alpha = 1$) and $T = 60$ days as mating season length. The square indicates predicted mating success in Lancaster Sound (LS) according to the estimated male and female densities.
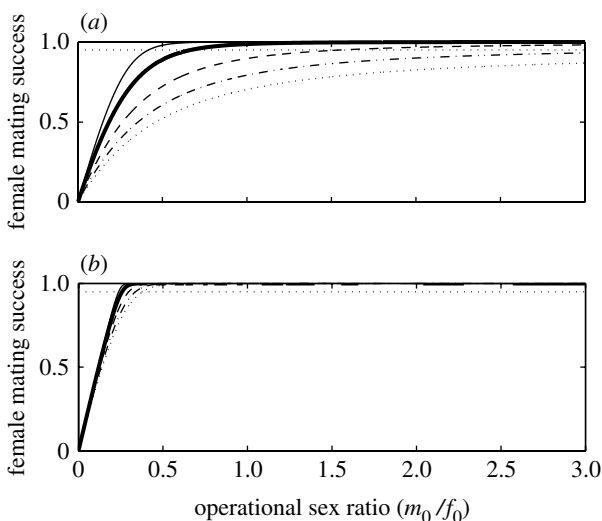

Figure 4. Female mating success as a function of the operational sex ratio m_0/f_0, with the overall density of breeding males and females, $m_0 + f_0$, held constant. Five representative densities are shown as follows: the estimated density in Lancaster Sound (solid thick line, 3.94 bears per 1000 km^2); as well as densities double that high (solid thin line, 7.88 bears per 1000 km^2); one-half as high (dashed line, 1.97 bears per 1000 km^2); one-third as high (dot-dashed line, 1.31 bears per 1000 km^2); and one-quarter as high (dotted line, 0.99 bears per 1000 km^2). The horizontal dotted line represents 95% mating success. (*a*) uses the maximum likelihood parameter estimates from Lancaster Sound ($\sigma = 2.05$ km^2/h, $\mu = (17.5$ days$)^{-1}$); (*b*) uses $\sigma = 20$ km^2/h, $\mu = (17.5$ days$)^{-1}$. Both (*a*) and (*b*) assume maximal male mating ability ($\alpha = 1$), and $T = 60$ days as mating season length.

the magnitude of the model parameters pair formation rate (σ), length of pair association ($1/\mu$), male mating ability (α) and mating season length (T; see electronic supplementary material). Similarly, female mating success, and thus the threshold operational sex ratio below which mating success declines, is density dependent

regardless of model parameters. However, the density dependence of female mating success becomes, weaker as pair formation rates increase, with mating success becoming less dependent on the overall density $m_0 + f_0$ and only dependent on the operational sex ratio m_0/f_0. For instance, using $\sigma = 2.05$ km^2 h^{-1}, $m_0/f_0 = 0.67$ is expected to yield 95% female mating success at the estimated density of available breeders in Lancaster Sound, but $m_0/f_0 = 4.43$ is required at one-third that density. However, with $\sigma = 20$ km^2 h^{-1}, 95% mating success is achieved with $m_0/f_0 = 0.26$ and $m_0/f_0 = 0.34$ at the two densities, respectively (figure 4).

All model parameters influence the quantitative predictions of female mating success. Increasing pair formation rate, increasing male mating ability, decreasing length of pair association and increasing mating season length all increase mating success. However, the non-linearity in the relationship between mating success and the operational sex ratio also becomes stronger with increasing pair formation rates, increasing male mating abilities, shorter pair associations and longer mating seasons, making a potential decline in mating success due to a lack of males both faster and more sudden (figure 4; figures S2*a*, S3*a* and S4*a* in the electronic supplementary material).

Mating success is most sensitive to pair formation rate, particularly at low densities, and somewhat sensitive to male mating ability, which becomes increasingly important at higher densities combined with balanced to female-biased operational sex ratios. By contrast, length of pair association (and thus the prevalence of polyandry) and mating season length have little influence on mating success. A detailed sensitivity analysis is provided in the electronic supplementary material.

5. DISCUSSION

Intensive sex-selective harvest of Canadian polar bear populations has led to concerns that a lack of males might eventually lead to reduced fertilization rates and subsequent population declines (Derocher *et al.* 1997; McLoughlin *et al.* 2005). Owing to the limited range of densities and sex ratios in natural populations, infrequent population inventories and because fertilization rates are not routinely measured, no data exist to describe the relationship between female mating success and male and female densities empirically. Therefore, we developed a mechanistic model to predict mating success from male and female densities. The model describes the pairing dynamics of a polar bear population during the mating season and was evaluated with the observed pairing data. Despite the lack of data on mating success, pairing data as used here are routinely collected during mark–recapture studies and can be used for model parametrization or validation.

Our approach of modelling the mating dynamics to predict female mating success differs from most previously proposed two-sex models, which usually focus on between-generation dynamics and assume a phenomenological birth function like the harmonic mean (Caswell & Weeks 1986; Lindström & Kokko 1998; Ranta *et al.* 1999) or phenomenologically describe mating success as a function of the operational sex ratio (Rankin & Kokko 2007). By contrast, we use a mechanistic process model

that describes the pairing dynamics of the mating season explicitly, focusing on the biological processes underlying mating success. Because our objective is the prediction of Allee effects, and predictions can be highly sensitive to model structure (Pascual *et al.* 1997; Wood & Thomas 1999; Stephens *et al.* 2002), such a mechanistic modelling approach is preferable over heuristic or semi-mechanistic models that include the Allee effect *a priori* or phenomenologically describe mating success as a function of male and female abundances (Boukal & Berec 2002), particularly in the absence of data to validate proposed functions. A similar approach was taken by Wells *et al.* (1990) and Veit & Lewis (1996), who also suggested second-order reproductive kinetics. However, our study not only extends their framework to the mating biology of polar bears, but is also the first to compare the predicted pairing dynamics with the observed pairing data, and thus to seek empirical validation for the proposed model structure. This step is crucial for predictive models, which should not only maximize realism, but also accurately fit historical data (Stephens *et al.* 2002; Haefner 2005).

The model explicitly incorporates pair formation and separation, the physical ability of males to locate and mate with several females and mating season length, which all influence female mating success. Mate-searching is an important variable in the reproductive dynamics of polar bears (Ramsay & Stirling 1986) and is implicitly incorporated through the rate of pair formation, which is simply the encounter rate between males and females multiplied by the probability of pair formation upon encounter (i.e. the degree of mate choice in the population). The sensitivity of mating success to pair formation rate supports the significance of efficient mate-searching for the mating dynamics of polar bears and further suggests a similarly important role of mate choice (Møller & Legendre 2001).

Regardless of parameter values, some qualitative predictions with profound management implications arise from the model. First, the threshold operational sex ratio, below which a component Allee effect of reduced female mating success is expected, is not constant but depends on the overall density of available breeders. The proportion of males needed to achieve high mating success increases with decreasing density, so that low-density populations might experience a component Allee effect even at the natural operational sex ratio of two to three males per available female. This density dependence arises from the need to search for mates and differs from findings in harem-breeding animals such as many ungulates, where the threshold operational sex ratio is relatively constant and depends on the male capacity to inseminate females (Ginsberg & Milner-Gulland 1994; Mysterud *et al.* 2002). Mate-searching is not an important component of the mating dynamics of harem breeders, so that these findings are consistent with our prediction that mating success becomes solely dependent on the operational sex ratio under high searching efficiencies.

Second, female mating success is a nonlinear function of the operational sex ratio, implying a sudden and rapid reproductive collapse if males are depleted below sustainable limits. Owing to this nonlinearity, already female-biased sex ratios, infrequent population inventories and the difficulty to determine the threshold operational sex ratio due to its density dependence, we recommend a precautionary harvesting approach. Currently observed high litter production rates (IUCN 2006) despite reduced male numbers should not be taken as evidence that populations are secure.

A cautionary example is given by the saiga antelope, where similar patterns as predicted here were observed. Despite heavy sex-selective poaching and a continuing depletion of adult males, female fertilization rates remained unaffected for a long time in this ungulate, but eventually collapsed in a sudden and nonlinear fashion when males were depleted below a critical threshold (Milner-Gulland *et al.* 2003).

The Lancaster Sound polar bear population with estimated 489 mature males and 451 mature available females seems relatively secure: 99% female mating success is predicted, with only 349 males required to fertilize 95% of females (assuming $\alpha = 1$). However, consider, for instance, a population reduction to one-third of this density (163 males and 150 females). Then, the current operational sex ratio of 1.08 yields only 81% mating success and 278 males would be needed to fertilize 95% of females. In other words, the current operational sex ratio would lead to a component Allee effect, illustrating the density dependence of mating success.

Quantitative predictions of mating success require relatively accurate parameter estimates, particularly of pair formation rate, the most sensitive model parameter. There is, however, uncertainty in our pair formation rate estimate due to the lack of pairing data from March. An early mating season start combined with large variability in the timing of female oestrus would let us underestimate pair formation rate due to lower densities of available females at any given time. Models incorporating such variability were explored, but not supported better by the data. Without data on pairings from March, the timing of oestrus or encounter rates between males and females, this matter cannot be explored further. However, underestimated pair formation rates would result in underestimated female mating success, making all our predictions conservative.

We might have overestimated pair formation rate by overestimating habitat area and thus underestimating densities, if bears aggregate due to habitat preferences (Stirling *et al.* 1993). However, such an overestimation would not affect mating success predictions in Lancaster Sound, because the same densities were used for parameter estimation and predictions. The matter would only become important if model parameters were used to predict mating success in other populations, which requires accurate estimates of both pair formation rate and male and female densities in these populations.

In contrast to searching efficiency, female mating success is insensitive to male mating ability at low densities, where the long time necessary for mate location makes it irrelevant whether males continue mate-searching after breeding pair dissolutions. However, strong negative effects of low male mating abilities were found at higher densities combined with balanced to female-biased operational sex ratios, where males and females easily find each other, but the ability of males to mate with several females becomes crucial (see electronic supplementary material). Because sex-selective harvest can also reduce mean male age (Taylor *et al.* in press *a*), and male mating ability is probably age dependent, a component

Allee effect could be initiated even at high densities with the estimated operational sex ratios maintained.

The simplifying assumptions of constant male and female densities, m_0 and f_0, throughout the mating season, as well as treating all but one male in multiple male breeding groups as solitary, are unlikely to affect our results. Variation in m_0 and f_0 may occur, for example, if originally unavailable females lose their litters and come into oestrus or if individuals are lost to harvest or natural mortality. However, these changes are probably small relative to total male and female numbers and would not significantly affect the pairing dynamics. Similarly, only few females were associated with several males when sampled. Moreover, because our objective is the prediction of Allee effects due to male scarcity, it is unnecessary to model multiple male breeding groups explicitly. Multiple male breeding groups probably become less frequent as male densities decrease.

In conclusion, we modelled the mating system of polar bears to identify circumstances leading to a component Allee effect of reduced female mating success. The model is intentionally simple, predicting mating success from male and female densities using only four parameters, with predictions insensitive to two of them. It incorporates, however, key biological mechanisms of the mating system and performs equally as well as more complex models in explaining the observed pairing data. To evaluate the generality of the model, it would be desirable to assess whether the model performs equally in other polar bear populations. Our model could next be coupled with a population dynamics model to explore whether and how a component Allee effect translates into a demographic Allee effect, and aid the development of optimal sex-specific harvesting strategies. Female mating success, as discussed here, is just one component of female reproductive success, which is further influenced by the rate of successful pregnancies as well as cub mortality. Furthermore, demographic stochasticity could lead to random fluctuations in the population sex ratio, and thus affect the number of males and females available for mating, particularly at low population sizes (Legendre *et al.* 1999; Stephens *et al.* 1999; Møller & Legendre 2001; Engen *et al.* 2003; Sæther *et al.* 2004). Such fluctuations would then, in turn, affect female mating success. This interaction merits further exploration.

Although we focus on the prediction of Allee effects in polar bears, our model is general enough to be applicable to other species, and it can easily be modified to incorporate characteristics of other mating systems. Here the key quantity remains the estimation of pair formation rates, that is, of encounter rates between males and females discounted for mate choice. If pairing data of the form used here are not available or unfeasible to collect, encounter rates could alternatively be estimated through different means such as intensive radio-telemetry programmes (Kovacs & Powell 2003) or separately modelled using movement speeds (Harcourt & Greenberg 2001).

This research adhered to the Association for the Study of Animal Behavior/Animal Behavior Society Guidelines for the Use of Animals in Research, the legal requirements of Canada and all institutional guidelines. We chemically immobilized and marked all bears following Animal Care Protocol No. 950005 of the University of Saskatchewan (under guidance of the Canadian Council on Animal Care).

APPENDIX A

The free parameters σ and μ were estimated by fitting the predicted pairing dynamics to the observed pairing data in Lancaster Sound using a maximum likelihood approach. Typical methods of fitting ordinary differential equations to data involve the method of least squares (Haefner 2005). In the present case, this would be appropriate if data on daily densities of males, females and pairs were available. However, as these densities are not available, we develop a method that is based on the proportion of males, females and pairs in each sample and involves a multinomial maximum likelihood function.

The model described by equations (3.1*a*)–(3.1*e*) and (3.2*a*)–(3.2*c*) predicts the respective densities of males and females that are available for mating ($M(t)$ and $F(t)$) and of those that are not ($M^*(t)$ and $F^*(t)$), as well as the density of breeding pairs $P(t)$ at any given time t. In the field, it is not possible to distinguish between bears that are available for mating and those that are not. Therefore, we summarized model predictions to give the total densities of solitary males and females at time t as $M(t) + M^*(t)$ and $F(t) + F^*(t)$, respectively. At any given time t, we could sample a solitary male, a solitary female or a pair from a sampling population whose density is predicted as $M(t) + M^*(t) + F(t) + F^*(t) + P(t)$. The proportions of solitary males, solitary females and pairs in this sampling population at time t are therefore predicted as

$$p_M(t) = \frac{M(t) + M^*(t)}{M(t) + M^*(t) + F(t) + F^*(t) + P(t)}$$

$$= \frac{M(t) + M^*(t)}{m_0 + f_0 - P(t)}, \qquad (A\,1a)$$

$$p_F(t) = \frac{F(t) + F^*(t)}{M(t) + M^*(t) + F(t) + F^*(t) + P(t)}$$

$$= \frac{F(t) + F^*(t)}{m_0 + f_0 - P(t)} \qquad (A\,1b)$$

$$p_P(t) = \frac{P(t)}{M(t) + M^*(t) + F(t) + F^*(t) + P(t)}$$

$$= \frac{P(t)}{m_0 + f_0 - P(t)}. \qquad (A\,1c)$$

Each bear can change between being solitary and paired throughout the mating season, so that captures should be regarded as sampling with replacement. Thus, assuming all

captures to be independent from each other, the probability of catching $m(t)$ males, $f(t)$ females and $p(t)$ pairs on a given sampling day t, given that there were $c(t) = m(t) + f(t) + p(t)$ captures, is multinomially distributed and predicted as

$$\Pr(m(t), f(t), p(t) | c(t))$$

$$= \frac{c(t)!}{m(t)! f(t)! p(t)!} (p_M(t))^{m(t)} (p_F(t))^{f(t)} (p_P(t))^{p(t)}, \quad \text{(A 2)}$$

where the probabilities of catching a male, a female or a pair, $p_M(t)$, $p_F(t)$ and $p_P(t)$, are given by (A 1a)–(A 1c). Given $c(t_i) = m(t_i) + f(t_i) + p(t_i)$ captures on day-of-the-year t_i, the negative log-likelihood function for pair formation rate, σ, and pair dissolution rate, μ, is given by

$$-L(\sigma, \mu | m(t_1), f(t_1), p(t_1), \dots, m(t_n), f(t_n), p(t_n))$$

$$= -\ln \left(\prod_{i=1}^{n} \Pr(m(t_i), f(t_i), p(t_i) | c(t_i)) \right), \quad \text{(A 3)}$$

where t_1 and t_n represent the first and last days of sampling, respectively. By minimizing this function, we obtained the respective parameter estimates (table 1).

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