THE ESTIMATION OF SURVIVAL AND LITTER SIZE OF POLAR BEAR CUBS

DOUGLAS P. DEMASTER,[1] National Fish and Wildlife Laboratory, 108 Zoology Building, Minneapolis, MN 55455
IAN STIRLING, Canadian Wildlife Service, 5320-122nd Street, Edmonton, Alberta T6H 3S5

Abstract: The mark/recapture analyses that are currently used to study polar bears (*Ursus maritimus*) generally underestimate the average number of cubs per litter and assume that the annual survival of cubs is unity. In this paper, a relationship among the number of yearlings per litter and 2-year-olds per litter is used to derive the survivorship of yearlings, which is then used to solve for the number of cubs per litter. When this relationship was applied to published population data from North America, the resulting estimated survival rates of yearlings ranged from 0.70 to 0.75, and the estimated average number of cubs per litter was between 1.70 and 1.98. These findings indicate that current estimates of sustainable yield for polar bear populations may be in error because the reproductive rate of adult females was likely to be underestimated, and the survival rate of cubs of the year was likely to be overestimated.

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Obtaining estimates of a sustainable yield requires information on age-specific rates of reproduction and survival. For polar bears, the age-specific rate of reproduction equals the product of the average number of litters produced per year times the average number of cubs per litter for a female of age *x*. Satisfactory estimates of litter production rates are derived from mark/recapture information (Stirling et al. 1975; unpubl. rep., Environ. Manage. Serv., Edmonton, 1978; Lentfer et al. 1980). However, current estimates of the average number of cubs per litter are unreliable. For example, the estimate by Lentfer et al. (1980) of the average number of cubs per litter was less than their estimate of the average number of yearlings per litter. In addition, they found fewer litters of cubs than of yearlings. Obviously, there are sampling biases because the average number of cubs per litter cannot be less than the average number of yearlings per litter and there must be at least as many litters of cubs as of yearlings. However, in lieu of suitable alternatives, the average number of cubs per litter is assumed to equal the average number of yearlings per litter.

Inherent in the assumption that the number of cubs per litter equals the number of yearlings per litter is the assumption that mortality of cubs is zero. Unfortunately, survival rates for cubs have not been estimated. Standard age class estimates of survival of cubs are not possible because, in most studies, a greater number of yearlings are captured than cubs, and sample sizes are typically too small for mark/recapture studies to be of use. An additional problem with assuming that mortality of cubs is zero is that the average number of yearlings per litter is consistently greater than the average number of 2-year-olds per litter (Stirling et al. 1975; unpubl. rep., Environ. Manage. serv., Edmonton, 1978; Lentfer, unpubl. rep., Alaska Fed. Aid Proj. W-17-4/5, 1976; Lentfer, et al. 1980). This implies that yearling mortality is greater than zero; therefore, it is unlikely that the mortality rate of cubs is zero. The purpose of this paper is to present a method that estimates yearling survival from the difference between the number of yearlings per litter and the number of 2-year-olds per litter, and then to show how to use this rate to estimate the number of cubs per litter.

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THE MODEL

The basis for estimating yearling survival is the relationship between the mean litter size of animals age i and age $i+1$. Estimates are derived by assuming that the survivorship of a cub is independent of litter size; i.e., cubs from litters of

[1] Present address: National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.

2 survive at the same rate as cubs from litters of 1. It is also necessary to assume that the survivorship of cubs is constant from year to year, and that litter sizes of 3 do not occur. Under these conditions, the expected litter size after 1 year is derived by a binomial process, except that litter sizes of zero are not observed.

For an initial litter size of 2 where s is the true annual survivorship of cubs, the probabilities, P, are:

$$P_2 \text{ (2 cubs survive 1 year)} = s^2$$

$$P_1 \text{ (1 cub survives 1 year)} = 2s(1-s)$$

$$P_0 \text{ (neither cub survives 1 year)} = (1-s)^2.$$

For a litter size of 1, the probability of 1 cub surviving is s.

The relationship between survival and the litter size of young of age i and $i+1$ is derived as follows:

$$N_{i+1} = 2n_i s^2 p_i + 2n_i s(1-s)p_i + n(1-p_i)s$$
$$= n_i s(1-p_i),$$

where

N_{i+1} = the number of cubs of age $i+1$,

n_i = the number of litters of age i, and

p_i = the proportion of litters with 2 cubs of age i.

The numbers of litters of age $i + 1$ is then:

$$n_{i+1} = n_i s^2 p_i + 2n_i s(1-s)p_i + n_i(1-p_i)s$$
$$= n_i s(p_i - sp_i + 1).$$

Therefore, if $E(X_i)$ is the estimated average litter size in year i, the expected value of the litter size after 1 year, given the initial proportion of litters with 1 and 2 members, and given an annual survivorship of s, is:

$$E(X_{i+1}) = \frac{n_i s(1+p_i)}{n_i s(p_i - sp_i + 1)}$$
$$= \frac{(1+p_i)}{(p_i - sp_i + 1)} \quad (1)$$

Because in any given year i,

$$E(X_i) = 2p_i + (1-p_i),$$

it can be easily shown that

$$p_i = \hat{X}_i - 1. \quad (2)$$

When Eq. (2) is incorporated into Eq. (1), the result is:

$$E(X_{i+1}) = (\hat{X}_i - s\hat{X}_i + s). \quad (3)$$

When estimates for X_i and X_{i+1} are available, Eq. (3) can be rewritten such that s is estimated by:

$$E(s) = \frac{(X_i - X_i X_{i+1})}{(X_{i+1} - X_i X_{i+1})} \quad (4)$$

In addition, if it is assumed that the survivorship of cubs equals the survivorship of yearlings, Eq. (4) can be rearranged to estimate the average litter size of cubs:

$$E(X_i) = \frac{sX_{i+1}}{(1 + sX_{i+1} - X_{i+1})} \quad (5)$$

APPLICATION OF THE MODEL

The survival rate of yearling polar bears, when estimated from the available data on the average number of yearlings per litter and 2-year-olds per litter, is relatively consistent between 4 different populations of polar bear (Table 1). These data indicate that yearling survival, given that the sow survives, is between 0.80 and 0.85. If adult survival equals 0.88 (Stirling et al., unpubl. rep., Environ. Manage. Serv., Edmonton, 1978; DeMaster et al. 1980), the estimated annual survivorship of yearlings is between 0.70 and 0.75. Estimates of yearling survival based on the ratio of successive age classes (number of yearlings/number of 2-year-olds) vary between 0.19 and 0.91 (Table 1). The wide range in survival estimates, based on the ratio of consecutive age classes, is primarily due to small sample sizes.

If it is assumed that the survival rate of cubs equals the survival rate of yearlings, Eq. (5) gives an estimated litter size for cubs of between 1.70 and 1.98. Considering that published estimates of the average number of cubs per litter ranged from 1.53 to 1.66 for this data set, it is clear that the proposed estimation procedure significantly departs from the previous approach.

The first assumption that the survival of cubs from litters of 1 equals the survival of cubs from litters of 2, is supported by data from 10 years of mark/recapture information on polar bears in Alaska, showing the proportion of cubs originally observed that were subsequently resighted as adults. Such resighting totaled 14 (20.0%) for 70 single-cub litters originally observed, and 31

Table 1. Observed litter sizes, from population studies of North American polar bears, and derived estimates of survival (from Eq. (4)) and original 1st-year litter size (from Eq. (5)). Yearling survival (y) is also estimated from the ratio of the number of yearlings to the number of 2-year-olds.

	Cubs			Yearlings			2-year-olds			Survival, *s*			Original litter size,
Data source	No. of litters	No. of cubs	Average litter size	No. of litters	No. of cubs	Average litter size	No. of litters	No. of cubs	Average litter size	Cubs	Yearlings	y	E(*X*)
Lentfer et al. (1980)	38	60	1.58	77	128	1.66	57	84	1.47	1.08	0.80	0.66	1.98
Stirling et al. (1975)	19	32	1.68	23	38	1.65	18	27	1.50	0.97	0.85	0.71	1.87
Stirling et al. (1980)	34	62	1.82	7	11	1.57	7	10	1.43	0.81	0.83	0.91	1.78
Stirling et al. (pers. comm.)	63	101	1.60	59	90	1.53	12	17	1.41	0.92	0.84	0.19	1.70

(15.2%) for 204 2-cub litters. These resighting rates are not significantly different ($X^2 = 0.88$, d.f. = 1). It is necessary to also assume that the survival of cubs is constant from year to year. There is no information to verify this assumption, but Stirling (unpubl. rep., Can. Wildl. Serv., 1978) reported that even in an unusually severe winter, the mortality of cubs was not significantly different from the mortality observed in more typical winters.

Finally, it is necessary to assume that litter sizes of 3 do not occur. Stirling et al. (unpubl. rep., Environ. Manage. Serv., Edmonton, 1978) and Lentfer et al. (1980) report litters of 3, but these are rare enough that in most areas of the Arctic their exclusion is not significant. Adoption is a potential mechanism that would also produce litters of 3. There is no evidence for adoption in any of the mark/recapture data from Alaska or Canada, and therefore we do not consider this a significant problem.

Predictions of the model seem reasonable where data exist to examine them. The consistent decrease in the number of yearlings per litter compared to the number of 2-year-olds per litter in the published literature indicates that mortality of yearlings is significant (Stirling et al. 1975, 1977; unpubl. rep., Environ. Manage. Serv., Edmonton, 1978; Lentfer, unpubl. rep., Alaska Fed. Aid Proj. W-17-4/5, 1978; Lentfer et al. 1980). It is not possible to estimate survival of cubs from existing data, but it has been speculated for other species of marine mammals that the survival of young of the year could be lower than that of any other age classes (Eberhardt 1977). It is therefore reasonable to expect cub survival to be less than unity.

There are 2 hypotheses that explain why published estimates for the mean number of cubs per litter are consistently low. The first states that litters of 1 may tend to be more mobile than litters of 2, and may therefore travel into ice types that investigators tend to search because of the increased visibility of polar bears. This would imply that the average distance between successive resightings of cub litters of 2 would be less than distances between successive resightings of cub litters of 1. A second hypothesis is that litters of cubs that are out in areas sampled by investigators experience higher mortality due to cannibalism by adult males than litters of cubs from areas less intensively studied. This implies that a near-shore sample of cub litters would have a higher mean litter size than an off-shore sample of cub litters. There are currently not enough data to test this hypothesis, but cannibalism of cubs by adult males has been reported (Stirling et al. 1975).

Additional data indicate that litter size estimates of 1.65 for cubs may be an underestimate. Data from zoos suggest that normally 2 young are born (Uspensky 1965; Harington 1968; Nunley 1977). In addition, polar bear populations in the Hudson Bay area typically have a mean number of cubs per litter between 1.8 and 2.0. However, this estimate of litter size may not be comparable with estimates of the number of cubs per litter from other areas because litters are larger in this area (Stirling et al. 1977) and litter size is determined from counts after families have left their dens but before they reach the sea ice.

Currently, estimates of the number of cubs per litter are generally assumed to equal estimates of the number of yearlings per litter. In addition, cub mortality is assumed to be insignificant. Because the average number of cubs per litter and the survival rate of cubs are important, statistics in the harvest models used to estimate sustainable yields, we recommend that the assumption concerning these statistics be reexamined. Small biases in either litter size or cub survival could result in serious errors in estimates of sustainable yields. For example, given a reproductive interval of 3.12 years (Lentfer, unpubl. rep., Alaska Fed. Aid Proj. W-17-4/5, 1976), a sex ratio of 1:1, and a mean cub litter size of 1.88, the annual rate of reproduction is approximately 0.30. However, if the mean cub litter size were 1.65, the rate of reproduction would be 0.26. The difference between 0.26 and 0.30 is critical for predicting sustainable harvests. Likewise, differences of roughly 0.15 in cub mortality are critical to the predictions of population models for polar bears. Given the current techniques in use, we feel that mortality of yearling polar bears is significant and that current estimates of the number of cubs per litter are negatively biased. We recommend that management practices be reviewed with these points in mind.

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