FERTILITY OF FEMALE MOOSE (*ALCES ALCES*) IN RELATION TO AGE AND BODY COMPOSITION

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ABSTRACT: We determined the fertility of female moose in central British Columbia, Canada, by examining a sample of 1198 reproductive tracts (183 of those with associated kidney mass and kidney fat mass measurements) from moose that had been shot by hunters between 22 Nov and 10 Dec, 1977 to 1995. We determined body composition by assuming kidney fat mass was an index of body fat and kidney mass was an index of body mass. Logistic regression indicated that the probability of becoming pregnant was related to kidney fat mass and age but not to kidney mass. Pregnancy rate was 19% for yearlings and greater than 73% for cows 2 to 10. The probability of having twins was related to kidney fat mass, age and kidney mass. The twinning rate was 14% in 2-year-old or older females. Fertility declined after age 13. Cows required 1.68 kg of kidney fat to a achieve a 50 % probability of conceiving twins but only 0.257 kg to a achieve a 50 % probability of conceiving a single fetus. Young females required greater fat reserves for pregnancy than did older females and the pregnancy threshold was inversely related to moose size. A higher fat threshold for pregnancy in young female moose may be an adaptation to increase their probability of surviving through the winter and producing a viable offspring. Variation in fertility among populations was more likely related to variation in the fat-fertility threshold than to variation in fat reserves.

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Ecological factors such as climate, weather, food quality, population density and predation risk affect physiological attributes like body mass and fat reserves which, in conjunction with other factors, affect fertility. If fertility is a good predictor of density, then wildlife managers could rely on fertility, which is usually easier to measure than density, as an indicator of a population's size in relation to ecological carrying capacity (KCC), the maximum number of animals that can be sustained by the resources of a particular environment (Caughley and Sinclair 1994:117). In female ungulates, some aspects of the relationship between ecology and fertility have been determined (Thomas 1982, Albon *et al.* 1983, 1991, Skogland 1990, Crête and Huot 1993, Jorgenson *et al.* 1993) and fertility has been shown to be related to an individual's body mass, fat, age and reproductive history (Ozoga and Verme 1982, Thomas 1982, Albon *et al.* 1986, Crête and Huot 1993, Allaye Chan-Mcleod *et al.* 1995, Hellegren *et al.* 1995, Gerhart *et al.* in press).

For female moose, Franzmann and Schwartz (1985), Boer (1992) and Gasaway *et al.* (1992) argued that adult twinning rate was an index of moose density relative to KCC. Sand (1996), however, showed that twinning was not necessarily related to the availability of browse but that moose living in relatively harsh and more seasonal environments needed to attain a greater body mass in order to have the same probability of twinning as moose living in milder climates. Fertility has been shown to be positively related to age (Markgren 1969, Sæther and Haagenrud 1983, Crichton 1992, Modafferi 1992 and Sand 1996) and body mass (Sæther

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and Haagenrud 1983, 1985, Sæther and Heim 1993, Sand 1996). McGillis (1972) found that pregnant moose usually have more fat than females that are not pregnant, but did not examine the relationship between fat and twinning.

In this paper, we document fertility in a sample of hunter killed female moose from central British Columbia, and examine the proximate and ecological correlates of those rates.

STUDY AREA

Our 22,000 km^2 study area was centered on Prince George, British Columbia, (53° 54'N x 122° 41' W). The terrain is flat to rolling with hundreds of small lakes and wetlands. Forests are mainly hybrid white-Engelmann spruce (*Picea glauca x engelmannii*) and subalpine fir (*Abies lasiocarpa*) with extensive successional stands of lodgepole pine (*Pinus contorta*). Fire and insect outbreaks, which were the dominant natural disturbances in the forest, have been largely eliminated and replaced by logging. Cut blocks, mostly created since the mid-1960's, are common throughout the area. Climate is influenced by prevailing westerly winds off the Pacific Ocean but with occasional periods of Arctic air in winter. The mean annual temperature is 3.3°C; -12°C in January and 14°C in July. The mean annual precipitation of 621mm, of which 63% falls as snow, is relatively evenly distributed throughout the year. Snow covers the ground from late-November through mid-April. Moose were rare in this region until early in this century. Between 1900 and 1930 numbers irrupted (Eastman 1977, Spalding 1990) and are now the most common ungulate. Moose are preyed on by black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*). In addition, 1340 ± 44 (SE) moose are shot each year (range 946 to 1691/yr, n = 19 years) with no trend over time ($r^2 = 0.0002$, $P = 0.95$). We believe that moose population number is stationary.

METHODS

All specimens were collected from moose shot by hunters between 22 November and 10 December during 1977 - 1995. From 1977 to 1990 we collected only the reproductive tract and an incisor tooth. Beginning in 1991 we also collected one kidney and its associated fat. In 1992 we collected a metatarsus. We rejected the data from specimens where the uterus was cut and a fetus could have been lost, or where it looked like any of the fat surrounding the kidney had been removed during collection.

We determined pregnancy and litter size by counting the number of embryos or fetuses. Because the minimum macroscopically detectable embryo length was 5 mm, the size reached approximately 25 days from date of conception (Markgren 1969), some late pregnancies may not have been detected e.g., cows conceiving after 28 October and shot on Nov 22. Age was determined from tooth annuli (Sergeant and Pimlott 1959), and we referred to moose age as of their previous birthday. We considered moose 2 years old or older to be adults.

We asked hunters to remove one kidney complete with the surrounding fat. Kidney fat index (KFI) was equal to the kidney fat mass (KFM) divided by kidney mass (KM), where kidney fat mass is the mass of all of the fat surrounding the kidney (not trimmed sensu Riney 1955). We considered kidney fat index and kidney fat mass to be indices of body fat. We considered kidney mass, metatarsus length and metatarsus mass to be indices of body mass. Kidney fat mass is probably a good index of body fat during the rut, because kidney fat mass was shown to be related to total body fat in caribou (Allaye Chan-Mcleod *et al.* 1995) and white-tailed deer (Finger *et al.* 1981). Stewart *et al.* (1977) showed that late November and early December kidney fat mass did not differ from kidney fat mass 2 months earlier. The validity of our assumption that kidney mass, metatarsus length and metatarsus mass are indices of moose body mass is unknown. However, kidney mass is positively related to injesta-free body mass in caribou (D. Heard unpublished data). We used logistic regression (PROC CATMOD, SAS Institute 1988) to determine the relationship between the binomial outcomes: 1) pregnant with 1 or 2 fetuses versus not pregnant (0 fetuses) and 2) twinning (pregnant with 2 fetuses) versus not pregnant with twins (fetuses = 0 or 1) and the independent variables for body composition, age and population composition.

We presented the relationship between the probability of being pregnant and the probability of having twins as described by Albon *et al.* (1986). Kidney fat mass was divided into 20 contiguous (5 percentile) subgroups. The proportion pregnant with one and with 2 fetuses was attributed to the median kidney fat mass of each subgroup and a logistic function fitted using PROC NLIN (SAS Institute Inc 1988).

Yearling pregnancy rate was estimated only when there were at least 4 yearlings in the yearly sample. Means are followed by their standard error. The moose growth curve was based on Schwartz and Hundertmark (1993). We used the Shapiro-Wilk statistic, *W*, from PROC UNIVARIATE (SAS Institute Inc 1988) to test for normality.

Composition of the moose population was estimated in December of each year by aerial survey using a Bell 206 helicopter. Flight routes were arbitrary within 12 different sampling units that made up the study area. Flying altitude and air speed varied to suit conditions. Moose were classified as calves, bulls or cows. Sex ratio statistics were determined using the Jackknife method.

We compared kidney fat mass to the duration of the vegetative growing season and previous winters' snow depths because Stewart *et al.* (1977) found that growing season was positively correlated with fall kidney fat and Mech *et al.* (1987) and McRoberts *et al.* (1995) found a significant inverse correlation between cumulative snow depths in 1, 2 and 3 previous winters and moose twinning rates. We assumed snow depths and temperatures recorded at Prince George (Ministry of Environment, Water Management Branch 1985 and Ministry of Environment, Lands and Parks files and Environment Canada files) reflected the general weather conditions throughout our study area. Stewart *et al.* (1977) defined the vegetative growing season as beginning when the sum of the daily maximum spring temperatures over 12.2°C exceeded 41.6°C and ending the first day that a fall temperature fell below -5°C. Snow depth accumulation for each winter was the sum of the January through April snow depths recorded on or about the first of each month.

RESULTS

We collected 1198 specimens for which we could determine age and litter size and for 183 of those specimens collected from 1991 to 1995, we also measured kidney mass and kidney fat mass. Although it was legal for hunters to shoot any antlerless moose, calves and yearlings were obviously under represented in our sample, but the age frequencies of older moose were similar to what one would expect in the live population (Fig. 1). There was no trend in the sampled age distribution over time for moose 2 years old or older (median age: $r = 0.024$, $P = 0.92$, $n = 19$).

Litter size was either 0, 1 or 2. None of the 52 calves was pregnant. Pregnancy rate (the proportion of moose that were pregnant) among 1 year old or older cows was 77% (887 / 1146, Fig. 2). Pregnancy rate in yearlings was 19% (23 / 121), significantly lower than in older cows ($G = 175$, $P = 0.0001$, df = 1). Pregnancy rate in 2 year old

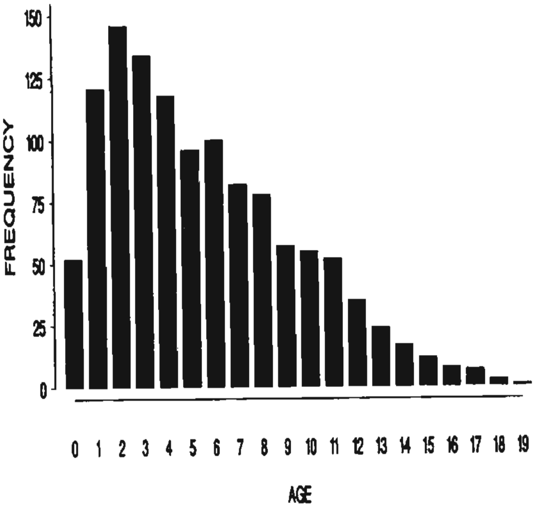

Fig 1. Age frequency of 1198 hunter killed cow moose shot in central British Columbia between 1977 and 1995.

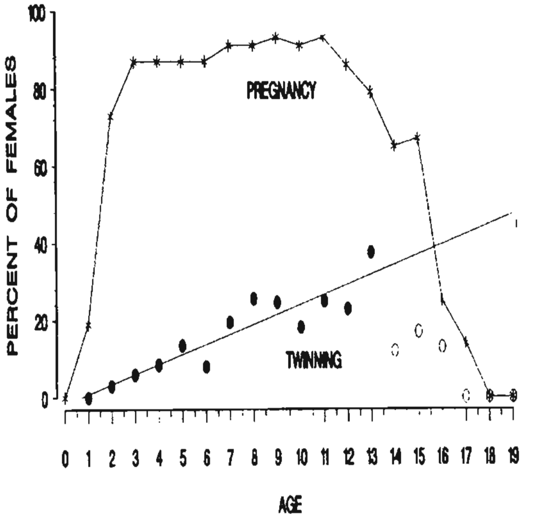

Fig 2. Age-specific pregnancy and twinning rates for cow moose in central British Columbia. Stars represent pregnancy rate. Solid and open circles represent twinning rate (TR). The regression line (TR = -1.72 + 2.58 AGE, $r^2 = 0.84$, $P = 0.0001$) was fit only to the solid circles.

cows (73%, 107 / 146) was not significantly lower than in older cows (80%, 705 / 879, $G = 3.46$, $P = 0.063$, df = 1). Pregnancy rate appeared to decline after age 11. None of the 121 yearlings was pregnant with twins. Twinning rate (TR) among adult cows was 14% (139 / 1025) and twinning rate showed a linear increase with age up to age 13 (TR = -1.72 + 2.58 AGE, $r^2 = 0.84$, $P = 0.0001$) and declined thereafter (Fig. 2). Adult twinning rates within a year were positively correlated with yearling pregnancy rates in that year (Fig. 3, $r = 0.63$, $P = 0.022$, $n = 13$).

Logistic regression indicated that both the probability of becoming pregnant and the probability of having twins was more closely related to kidney fat mass than to kidney fat index (for pregnancy, $\chi^2_{KFM} = 13.08$, $P = 0.0003$ and $\chi^2_{KFI} = 1.08$, $P = 0.30$; for twinning, $\chi^2_{KFM} = 16.65$, $P < 0.0000$ and $\chi^2_{KFI} = 8.53$, $P = 0.0035$). Therefore we used only kidney fat mass in subsequent analyses. Kidney fat mass was significantly lower in calves (0.057 ± 0.0089 kg) than in older moose (0.720 ± 0.035 kg, $F_{1,182} = 36.3$, $P = 0.0001$) but there was no relationship between age

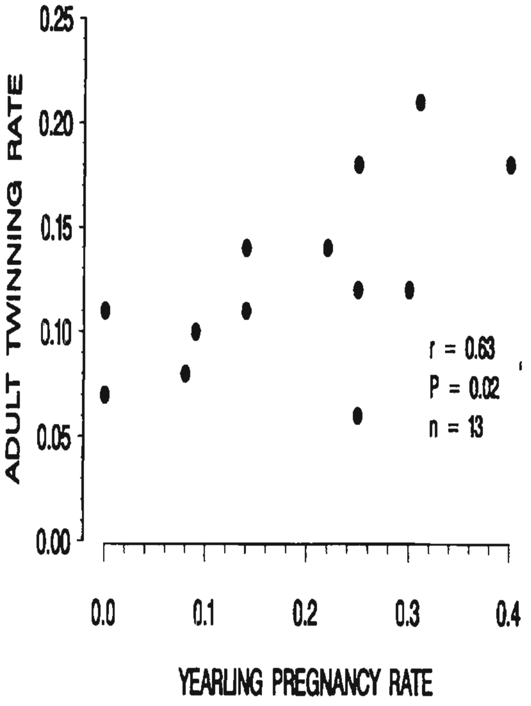

Fig 3. Correlation between annual adult twinning and yearling pregnancy rates for a sample of hunter killed cow moose shot between 1977 and 1995 in central British Columbia.

and kidney fat mass in cows one year old or older ($P = 0.36$).

Kidney mass appeared to be an index of body mass. Kidney mass increased from a mean of 0.269 ± 0.078 kg as calves to an asymptote at age 5 of 0.529 ± 0.098 kg., it fit a von Bertalanfy growth curve ($KM(g) = 529\ (1 - 0.333\ (EXP\ \{ -0.554\ (AGE + 0.966)\}))^3$, $F_{2,181} = 3582, P < 0.0000$) and it was correlated with metatarsus length (r = 0.77, P = 0.0001, n = 29) and metatarsus mass (r = 0.83, P = 0.0001, n = 29). Kidney mass was correlated with kidney fat mass (r = 0.51, P = 0.0001, n = 325).

Adult sex ratio showed no trend with time ($r^2 = 0.12$, $P = 0.15$, $n = 18$) averaging 49.1 ± 0.71 bulls to 100 cows (Table 1).

Logistic regression indicated that the probability of becoming pregnant was positively related to kidney fat mass ($\chi^2 = 24.7$, $P = 0.0001$) and age ($\chi^2 = 18.4$, $P = 0.0001$), for moose less than 14 (see Fig. 2), but not to kidney mass ($\chi^2 = 0.0006$, $P = 0.98$), year of collection ($\chi^2 = 0.12$, $P = 0.72$), population sex ratio ($\chi^2 = 0.014$, $P = 0.91$) or the interaction of those variables. The probability of becoming pregnant was related to kidney fat mass by the logistic curve ($Y = 88 / \{ 1 + EXP\ (-14.3\ (KFM - 0.238))\}$, $F_{3,17} = 321$, P = 0.0001, Fig. 4).

If one sex were less costly to produce than the other, then pregnancy probability may be related to fetus sex but this was not the case. Fetal sex ratio did not vary from

Table 1. Moose population sex ratio, sum of monthly snow depths from January through April and length of the vegetative growing season as defined by Stewart *et al.* (1977) in central British Columbia between 1976 and 1995.

Year	Bulls:100 cows	SE	Number of sample units	Number of moose	Snow depth (cm)	Growing season (days)
1976/77	-	-	-	-	129	-
1977/78	58	2.2	6	685	151	-
1978/79	49	6.0	4	176	256	-
1979/80	45	1.5	6	390	137	-
1980/81	73	25.1	2	161	62	184
1981/82	.	.	0	0	367	165
1982/83	44	1.0	8	678	116	156
1983/84	50	2.4	8	637	107	149
1984/85	47	1.1	7	1027	206	141
1985/86	38	2.5	5	420	130	143
1986/87	63	0.7	6	1104	131	164
1987/88	49	2.0	7	968	150	161
1988/89	50	0.7	6	1170	196	146
1989/90	40	1.8	9	1170	167	173
1990/91	39	2.2	8	945	274	163
1991/92	51	0.9	10	1019	53	187
1992/93	51	2.7	6	897	161	140
1993/94	53	3.1	6	587	183	138
1994/95	48	2.9	7	949	89	187
1995/96	36	2.0	5	843	-	177

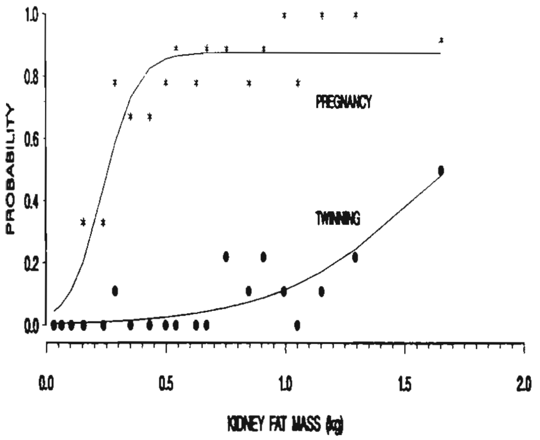

Fig 4. Relationship between kidney fat and pregnancy and twinning probabilities for cow moose in central British Columbia. Curves were fit by logistic regression to points representing the proportion of consecutive 5 percentiles of kidney fat mass for cows that were pregnant (stars) and had twin fetuses (dots).

50:50 (χ^2 = 0.74, *P* = 0.39, females = 280, males = 290). Logistic regression indicated that the probability of producing a daughter was not related to kidney fat mass (χ^2 = 0.78, *P* = 0.37), kidney mass (χ^2 = 2.0, *P* = 0.16), age (χ^2 = 0.50, *P* = 0.48) or year of collection (χ^2 = 2.3, *P* = 0.13).

The probability of conceiving twins was positively related to kidney fat mass (χ^2 =12.2, *P* = 0.0005), kidney mass (χ^2 =5.8, *P* = 0.016) and age (χ^2 =5.2, *P* = 0.023) for moose less than 14 years old. Neither year of collection (χ^2 =0.57, *P* = 0.45), sex ratio (χ^2 =0.21, *P* = 0.64) nor interactions among independent variables were significantly related to the probability of twinning. Cows required 1.68 kg of kidney fat to a achieve a 50 % probability of conceiving twins but only 0.257 kg to a achieve a 50 % probability of conceiving a single fetus (Fig. 4). The probability of conceiving twins was related to kidney fat mass by the logistic curve ($Y = 88 / \{ 1 + EXP (-3.21 (KFM - 1.59))\}$, $F_{2,18}$ = 36.8 *P* = 0.0001), assuming the same asymptote as for pregnancy, which was 88%.

To demonstrate the effect of age on litter size in addition to the effect of kidney fat mass, we plotted the kidney fat mass-litter size probabilities for moose 0 to 5 years old and 5 years old or older using 10 percentile increments (Fig. 5). Five was the median age. For a given amount of fat, older cows were more likely to be pregnant and, especially at high fat levels, more likely to conceive twins than younger cows. To show the effect of kidney mass on twinning, 10 percentile kidney fat mass increments were subdivided into heavy and light kidney masses at the median kidney fat mass of 0.623 kg. The probability of conceiving twins was greater for cows with relatively heavy kidneys (Fig. 6) and the mean kidney mass of cows with twins was significantly higher than kidney mass of other 2 year old or older cows (*t* = 4.14, df = 145, *P*=0.0001) .

When we classified those moose with more than 0.257 kg of kidney fat as pregnant (i.e., having more than a 50% chance of being

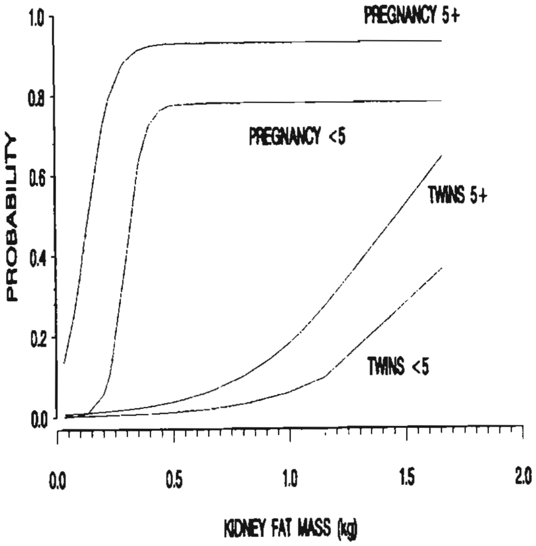

Fig 5. Effect of age on the relationship between litter size and kidney fat mass for cow moose classified as < 5 years old or 5 years old or older. Curves were fit by logistic regression to points representing the proportion of consecutive 10 percentiles of kidney fat mass for each age class that were pregnant (upper lines) or had twin fetuses (lower lines).

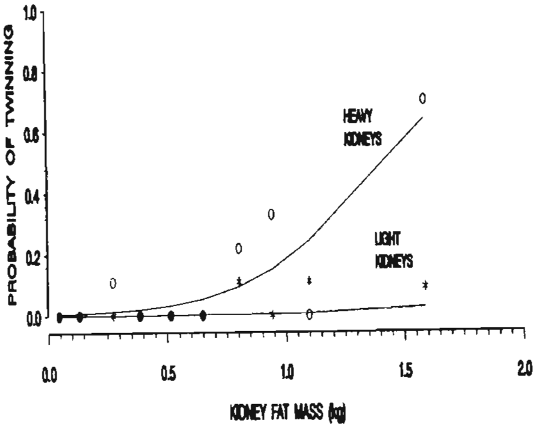

Fig 6. Effect of kidney mass on the relationship between twinning probabilities and kidney fat mass. Curves were fit by logistic regression to points representing the proportion of consecutive 10 percentiles of kidney fat mass for cow moose with relatively heavy kidneys (circles) or relatively light kidneys (stars).

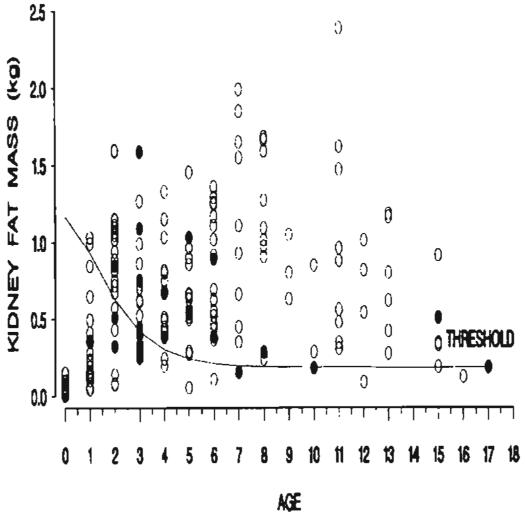

Fig 7. Kidney fat mass threshold for pregnancy, based on the inverse of moose growth in relation to moose age. Circles represent cows that were classified correctly using that threshold; circles above the line represent cows that were pregnant (n = 114) and circles below the line represent cows that were not pregnant (n = 46). Dots represent cows that were misclassified, dots above the line represent cows that were not pregnant (n = 14) and dots below the line represent cows that were pregnant (n = 9).

pregnant, Fig. 4) and those with less than 0.257 kg of kidney fat as not pregnant, only 14% (26 of 183) of the moose were misclassified. As shown in Fig. 5, the 50% probability threshold was age dependent, 0.322 kg for cows < 5 and 0.138 kg for cows 5 years old or older. Using those 2 thresholds, the number misclassified dropped to 23 (13%). We had too few data to estimate the 50% pregnancy threshold for each age but a curve based on the inverse of the moose growth curve provided a continuously declining pregnancy threshold that fit the data equally well. Twenty-three individuals were also misclassified (Fig. 7) with the distances of those 23 kidney fat masses from that threshold being normally distributed (W = 0.948, P = 0.26).

The probability of having twins was 50% when kidney fat mass was 1.68 kg (Fig. 4). The 4 cows with at least that much fat all had twins, but the 12 other cows with twins were misclassified (Fig. 8). Because all the cows that did not conceive twins were classified correctly, the total number misclassified was 12 of 183 (7 %). Using kidney fat index rather than kidney fat mass (because twinning was related to both kidney fat mass and kidney mass) did not reduce the number misclassified.

Given that annual estimates of yearling pregnancy rates and adult twinning rates were correlated among years (r = 0.72, P = 0.020, n = 10), and that kidney fat mass had the greatest influence on litter size, we looked for annual variation in environmental conditions that might be related to kidney fat mass. Multiple linear regression indicated that kidney fat mass was positively related to snow depth during the previous winter (r^2 = 0.073, P = 0.0001, n = 216), but not to vegetative growing season nor to snow depths during winters 2 or 3 years previously (P > 0.11). Even though we found a relationship between snow depth and kidney fat, r^2 was very low, and neither pregnancy rate nor twinning

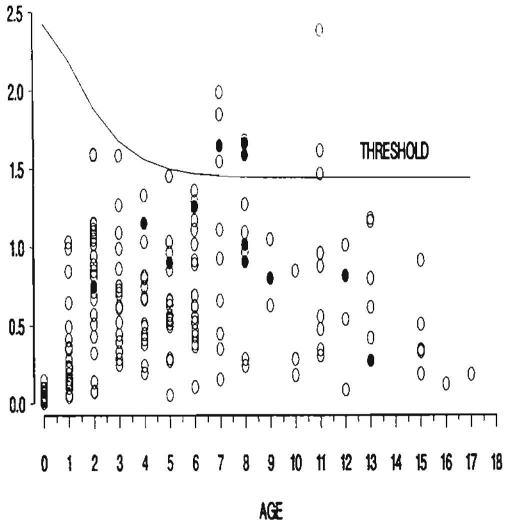

Fig. 8. Kidney fat mass threshold for twinning, based on the inverse of moose growth in relation to moose age. Circles represent cows that were classified correctly using that threshold, circles above the line represent cows that had twins ($n = 7$) and circles below the line represent cows that did not have twins ($n = 164$). Dots represent cows that were misclassified, dots above the line represent cows that did not have twins ($n = 3$) and dots below the line represent cows that had twins ($n = 9$).

rate was related to the previous winter's snow depth when we considered all 19 years of data, $P_{\text{pregnancy rate}} = 0.73$, $P_{\text{twinning rate}} = 0.93$).

DISCUSSION

In female moose, pregnancy was positively related to kidney fat mass and age, up to age 13 when moose showed reproductive senescence. Twinning was positively related to kidney fat mass, kidney mass and age, up to 13. Much more fat was required to produce twins than a single fetus. Young females required greater fat reserves for pregnancy than did older females, and the pregnancy threshold was inversely related to moose size. Sand (1996) found that age and body mass were related to moose fertility in Sweden, but he did not measure body fat. If kidney mass was an accurate index of body mass, then it appears from our data that body fat is a more important determinant of moose fertility than is body mass, as has been shown for caribou (Ouellet *et al.* 1997, Gerhart *et al.* 1997).

Sand (1996) suggested that a higher mass threshold for pregnancy in young females may represent a trade-off between early maturation and future growth. We suggest that the trade-off is between early maturation and survival, rather than future growth, because fertility was more closely related to fat than mass. Younger and smaller moose probably have greater costs moving and foraging in snow, and the probability of dying from starvation and producing a viable offspring is probably related to fat reserves. Early maturation reduces growth rate (Sæther and Haagenrud 1985, Sand and Cederlund 1996), but does not appear to reduce fertility later in life, because early maturation was not related to adult mass (Sand and Cederlund 1996), populations with large yearlings had large adults (Sæther and Haagenrud 1985), and yearling pregnancy was positively correlated with adult twinning rate (Fig. 3, Boer 1992).

The same fat-survival trade-off probably accounts for the higher fat threshold for twinning. Cows conceiving twins would have greater gestation and lactation costs and would require greater fall fat reserves than cows with a single fetus, for both to have the same probability of dying from starvation and producing viable offspring.

Moose fertility varies substantially among populations (Franzmann and Schwartz 1985, Sæther and Haagenrud 1985, Boer 1992, Gasaway *et al.* 1992, Sand 1996) and fertility is often much greater than what we found in central British Columbia. The mean adult twinning rate equaled 49 ± 5.7 % (range = 4 % to 90 %) in 25 populations cited by Franzmann and Schwartz (1985), Boer (1992) and Gasaway *et al.* (1992), compared to 14 % in this study. Although those studies did not provide age specific twinning rates, population differences were too great to be accounted for solely on the basis of variation in age structure. Variation in fertility among populations could result from variation in the accumulation of fat reserves, from variation in the fat-fertility threshold, or both.

We found a weak positive relationship between snow depth and fat accumulation. Mech *et al.* (1987) and McRoberts *et al.* (1995) concluded that, on Isle Royale, moose twinning rates and maternal body condition were inversely related to winter snow depths, and that the effects of snow accumulated over the 3 previous winters. We found no relationship between snow depth and fertility. Our data were not directly comparable to those presented by for Isle Royale, because we determined in utero twinning rates just after conception and before winter, whereas Mech *et al.* (1987) looked at twinning in the live population after the winter and after post-partum mortality could have occurred. Nonetheless, because Mech *et al.* (1987) were postulating cumulative nutritional effects from previous winters, we would still have expected to find a relationship if one existed in our study area. Our data therefore support Messier's (1991) conclusion that cumulative winter snow depths have relatively minor effects on moose twinning rates.

Franzmann and Schwartz (1985), Boer (1992) and Gasaway *et al.* (1992) argued that high moose densities would lead to lower fat accumulation and lower adult twinning rates. We thought it unlikely that intraspecific competition was high enough in central British Columbia to severely limit per capita food availability, because moose densities are invariably well below KCC wherever moose populations are hunted and preyed on by black bears, brown bears and wolves (Gasaway *et al.* 1992, Messier 1994). With both low twinning rates and low densities relative to KCC, it does not appear that competition for food was limiting fat accumulation.

Fat accumulation may be limited by food quality, rather than food quantity, even in a population below KCC. Daily intake rates of moose and other herbivores are ultimately constrained by processing time and gut clearance rates (Belovsky 1978, Wilsmhurst and Fryxell 1995). Low quality foods have slower digestive processing rates, thus limiting energy intake and fat accumulation by individual moose even when food biomass is high and there is enough low quality food to support more moose. Where energy intake is limited by food quality, fat reserves at the end of summer will also be related to energy requirements, primarily lactation costs, which have been shown to reduce fall fat reserves and the probability of pregnancy in red deer and caribou (Albon *et al.* 1986, Gerhart *et al.* in press).

Predation-sensitive foraging refers to the behaviour of animals that exploit food with the lowest risk of predation first and, as food becomes limiting, take greater risks to obtain more food. If high food quality patches have a higher predation risk, moose will tend to avoid those areas. Foraging risks for moose would depend on the number of predator species, predator densities, and the distribution of food relative to secure habitat. Predation-sensitive foraging (Sinclair and Arcese 1995) has been shown for moose in winter (Edwards 1983, Stephens and Peterson 1984) and for other cervids in summer (Festa-Bianchet 1988, Berger 1991, Heard 1992, Heard *et al.* 1996). The similarities of adult moose pregnancy rates over a wide variety of densities, geographic areas and environmental conditions (Boer 1992) suggests to us that in most places food of sufficient quality exists and moose are willing, and able to do whatever is necessary to achieve the fat threshold for pregnancy, possibly by incurring increased predation risk. The wide variation in twinning rates could be explained by moose not being willing to incur an increased predation risk in order to accumulate enough fat to conceive twins. Variation in fat accumulation and fertility among populations may therefore be related to variation in predation risk.

The threshold for maturity in most animals is not fixed but varies with environmental conditions (Albon *et al.* 1983, Skogland 1990, Bernardo 1993, Festa-Bianchet *et al.* 1995, Ouellet *et al.* 1997). Sand (1996) found that the fat-fertility threshold varied among moose populations, and that climate had a greater effect than food availability on fertility in populations that were below KCC. Moose living in relatively harsh and more seasonal environments had a higher mass-fertility threshold than moose living in milder climates. It seems reasonable to assume that moose living in relatively harsh environments would also have a higher fat-fertility threshold. In general, fall fat-fertility thresholds appear to be related to an animal's expected winter energy balance. Higher fat thresholds should be expected whenever energetic costs are higher e.g., for populations in harsh environments, for populations with low food quality or quantity, for individuals carrying twins, and for younger and smaller animals with greater foraging costs.

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