Conservation Biology

*Conservation Practice and Policy*

# Estimation of Body-Size Traits by Photogrammetry in Large Mammals to Inform Conservation

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**Abstract:** *Photography, including remote imagery and camera traps, has contributed substantially to conservation. However, the potential to use photography to understand demography and inform policy is limited. To have practical value, remote assessments must be reasonably accurate and widely deployable. Prior efforts to develop noninvasive methods of estimating trait size have been motivated by a desire to answer evolutionary questions, measure physiological growth, or, in the case of illegal trade, assess economics of horn sizes; but rarely have such methods been directed at conservation. Here I demonstrate a simple, noninvasive photographic technique and address how knowledge of values of individual-specific metrics bears on conservation policy. I used 10 years of data on juvenile moose (*Alces alces*) to examine whether body size and probability of survival are positively correlated in cold climates. I investigated whether the presence of mothers improved juvenile survival. The posited latter relation is relevant to policy because harvest of adult females has been permitted in some Canadian and American jurisdictions under the assumption that probability of survival of young is independent of maternal presence. The accuracy of estimates of head sizes made from photographs exceeded 98%. The estimates revealed that overwinter juvenile survival had no relation to the juvenile's estimated mass (*$p < 0.64$*) and was more strongly associated with maternal presence (*$p < 0.02$*) than winter snow depth (*$p < 0.18$*). These findings highlight the effects on survival of a social dynamic (the mother-young association) rather than body size and suggest a change in harvest policy will increase survival. Furthermore, photographic imaging of growth of individual juvenile muskoxen (*Ovibos moschatus*) over 3 Arctic winters revealed annual variability in size, which supports the idea that noninvasive monitoring may allow one to detect how some environmental conditions ultimately affect body growth.*

**Keywords:** conservation policy, moose, muskoxen, orphans, overwinter survival, photogrammetry

Estimación de Atributos de Tamaño Corporal por Fotogrametría en Mamíferos Mayores para Informar a la Conservación

**Resumen:** *La fotografía, incluyendo imágenes remotas y cámaras trampa, ha contribuido sustancialmente a la conservación. Sin embargo, el potencial de uso de la fotografía para entender la demografía e informar a los políticos es limitado. Para tener valor práctico, las evaluaciones remotas deben ser razonablemente precisas y ampliamente aplicables. Los esfuerzos previos para desarrollar métodos no invasivos para estimar el tamaño de atributos han sido motivados por un deseo de responder a preguntas evolutivas, medir crecimiento fisiológico o, en el caso de comercio ilegal, evaluar la economía de cuernos de diferentes tamaños; pero esos métodos raramente han sido utilizados en conservación. Aquí demuestro una técnica fotográfica sencilla, no invasiva y muestro como el conocimiento de los valores de medidas individuales proporciona soporte a las políticas de conservación. Utilicé datos de 10 años de alces (*Alces alces*) juveniles para examinar si el tamaño corporal y la probabilidad de supervivencia están correlacionados positivamente en climas fríos. Investigué sí la presencia de madres mejoró la supervivencia juvenil. Esta relación es relevante para las políticas porque la cosecha de hembras adultas ha sido permitida en algunas jurisdicciones canadienses y norteamericanas bajo*

*Paper submitted July 12, 2011; revised manuscript accepted January 13, 2012.*



*Conservation Biology*, Volume 26, No. 5, 769–777
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DOI: 10.1111/j.1523-1739.2012.01896.x

*el supuesto de que la probabilidad de supervivencia de jóvenes es independiente de la presencia materna. La precisión de las estimaciones del tamaño de la cabeza hechas a partir de fotografías excedió 98%. Las estimaciones revelaron que la supervivencia juvenil a la hibernación no tuvieron relación con la masa juvenil estimada (*$p < 0.64$*) y estuvo más estrechamente asociada con la presencia materna (*$p < 0.02$*) que con la profundidad de la nieve (*$p < 0.18$*). Estos resultados resaltan los efectos de una dinámica social (la asociación madre-juvenil) sobre la supervivencia en lugar del tamaño corporal y sugieren que un cambio en la política de cosecha incrementará la supervivencia. Más aun, las imágenes fotográficas del crecimiento individual de bueyes almizcleros (*Ovibos moschatus*) en 3 inviernos árticos revelaron variabilidad anual en el tamaño, lo cual sustenta la idea de que el monitoreo no invasivo puede permitir la detección del efecto de algunas condiciones ambientales sobre el crecimiento corporal.*

**Palabras Clave:** alce, buey almizclero, fotogrametría, huérfanos, políticas de conservación, supervivencia a la hibernación

## Introduction

Photogrammetry—the determination of properties of objects in photographs—has contributed insights about the size of morphological features (e.g., tails, horns, and skeletal dimensions) of individuals in taxonomic groups ranging from primates, to ungulates, to whales (Ratnaswamy & Winn 1993; Minn 1997; Durban & Parsons 2006). However, photogrammetry has rarely been used to inform conservation policy. I used photogrammetric data to examine whether there is a link between individual growth rates in wild ungulates and conservation policy. In Arctic and boreal biomes, for instance, where temperatures are rising at twice the rate as elsewhere (IPCC 2007), fundamental uncertainties exist about how warming will affect populations of hunted species such as moose (*Alces alces*), caribou (*Rangifer tarandus*), and muskoxen (*Ovibos moshchatus*) (Post et al. 2009). Given the competition between subsistence hunters and native carnivores for prey and tension among stakeholders regarding hunting regulations (Adams et al. 2008), it seems of value to understand how such sources of food may be affected by weather, nutrition, predation, and other factors (Forchhammer et al. 2002; Bowyer et al. 2005). Estimates of prey size associated with vital rates (e.g., pregnancy or survival) that ultimately affect population trajectories can help inform management decisions that include the modification of harvest levels or strategies.

My specific aims were 3-fold. First, I sought to describe conservation efforts in which photogrammetrically derived estimates of body size are linked to individual survival. I did this for moose in the wild. Moose are a food source of importance to subsistence hunters in Asia, Europe, and North America, and photogrammetrically derived estimates of their size as juveniles can inform harvest policies. I assessed the extent to which variation in body size and snow depth was associated with juvenile survival because U.S. state and Canadian provincial governments permit some harvest of adult females irrespective of juvenile presence. If the probability of survival of juveniles is increased by attaining a relatively large size rather than maternal presence, then hunting of mothers will have less of a demographic effect than if juvenile survival depends on maternal presence. If the management goal is to maximize juvenile survival, but the mortality of juveniles is exacerbated by the loss of their mothers, then a change in harvest policy may be required to maximize survival. Second, given the high rate of climate change in northern biomes, I used the case of muskoxen to examine whether photogrammetrically derived estimates of head size are useful as a proxy of the response of skeletal growth to environmental variation. Third, I explored advantages and limitations of photogrammetry in other systems and with other species.

Modern photography enables assessment of the size of morphological features, some of which (e.g., horns and skeletal dimensions [Bergeron 2007; Rothman et al. 2008]) are associated with weather and nutrition. For instance, size and mass of young ungulates are sensitive to annual weather conditions (Clutton-Brock et al. 1982; Adams 2005), and it is possible to compare how growth is associated with vital rates on the basis of data collected through noninvasive monitoring. In juvenile bison, for example, head size is positively correlated with body mass; ~85% of the variance in weight is explained by 2 head dimensions (Berger & Cunningham 1994). Hence, as a starting point, I explored whether patterns of juvenile growth can be linked through demographic models of climate and population change (Keech et al. 2000). During projects in the 1990s, Testa and Adams (1998) and I (Berger et al. 1999, 2001) showed that head size was a reliable predictor of body mass in juvenile moose. Thus, photographs of morphological traits and their annual variation may inform management policy.

## Methods

### Photogrammetry Measures in Captive and Wild Populations

In March 1998, Testa (2004) immobilized, measured head width (indexed as distance between orbits of the eyes) and length (tip of nose to occipital condyle), and weighed 29 yearling female Alaskan moose. Testa and I

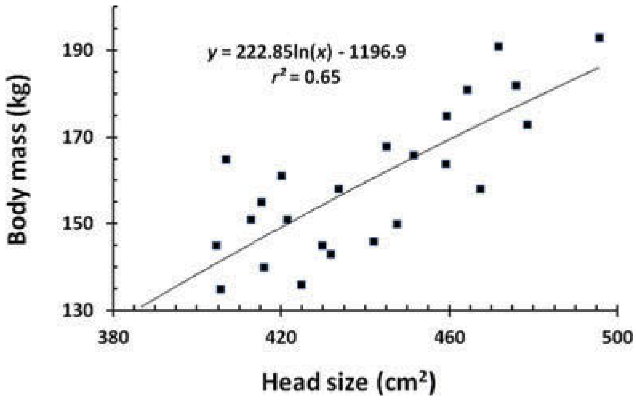


*Figure 1. Relation between head size and body mass (p < 0.001) of 10-month-old female moose in the Talkeetna Mountains, Alaska (U.S.A.).*

(unpublished) subsequently confirmed a relation between body mass and head size ([0.5]head width ∗ head length) (Fig. 1).

To explore whether an animal's size can be estimated without handling, I assessed the reduction in size (length between fixed points on an object in digital photographs) as a function of photodistance (i.e., distance from the camera to the subject). I measured the gap between horn tips on photographs of a muskoxen skull that I took at 5-m intervals from 10 to 100 m (Fig. 2a). Although actual space between tips is constant, there is a distance effect with photographs (i.e., as distance from the object increases, the object appears smaller), which I accounted for by scaling object size as 400 mm (i.e., focal length/distance from camera to subject). I used a Nikon D-300 camera and AF-VR 80–400 mm F4.5–5.6 lens (Nikon, Tokyo) with focal length for photographs fixed at 400 mm with a rangefinder (Master CRF 1000, Leica, Allendale, New Jersey) to generate object size and distance to subject. I measured object size in photographs with digital calipers (Iconico, New York, New York).

I examined the relation between head dimensions and body mass by measuring 53 captive muskoxen 0.8–18 years old at the Large Animal Research Station, University of Alaska, Fairbanks. I photographed these muskoxen at various distances, and they were weighed within 3 days of the photographs being taken (Peltier & Barboza 2003). White hair on the heads of young animals led to some ambiguity in locating occipital condyles (Fig. 3).

The relation between total (2-dimensional) head size and body mass was significant ($Y = 129.52 \ln [x] - 606.35$; $r^2 = 0.86$; $p < 0.001$) for 1- to 3-year-olds independent of gender. However, with all animals included, the amount of variance explained was nearly halved ($r^2 = 0.44$; $Y = 73.001 \ln[x] + 327.56$). For adults only, there was essentially no relation ($r^2 = 0.03$; $Y = -23.168 \ln[x] + 528.45$) between head size and mass. Therefore, I used only juvenile muskoxen head size, not mass, because I wanted to determine whether photograph-derived estimates could represent size and because of the uncertainty in extrapolating size-mass relations from captive to wild animals.

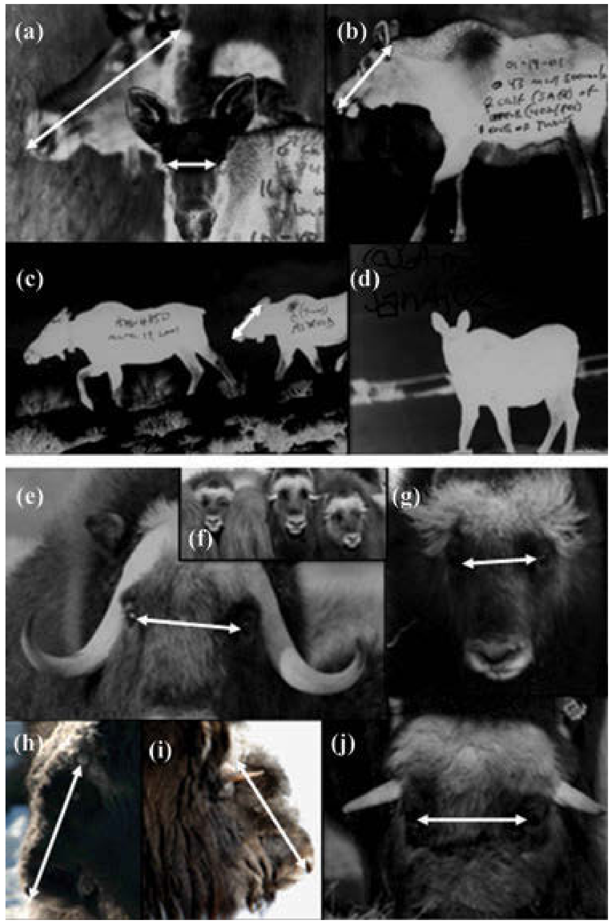


*Figure 2. Comparison of usable and unusable photographs of moose and muskoxen (size of photographs adjusted to fit schematic) (wild moose a–d, muskoxen e–j): (a) ≥4-month-old male juvenile (forward facing) 16 m from camera, usable; juvenile's mother (profile in distance), unusable because distance from camera was not measured, (b) 7-month-old female juvenile at 43 m, usable; (c) 10-month-old male juvenile at 48 m, usable; (d) female at 63 m, unusable; (e) wild 3-year-old male at 22 m, usable; (f) wild 1-year-old male, 2-year-old female, and 1-year-old male at 24 m, usable; (g) wild 1-year-old female at 18 m, usable; (h) wild 1-year-old male at 21 m, usable; (i) captive 2-year-old female at 25 m, usable; (j) captive 2-year-old female at 14 m, usable (all moose were wild and were photographed in Jackson Hole, Wyoming [U.S.A.]; captive muskoxen from University of Alaska and wild muskoxen were from Bering Land Bridge and Cape Thompson regions, Alaska [U.S.A.]).*

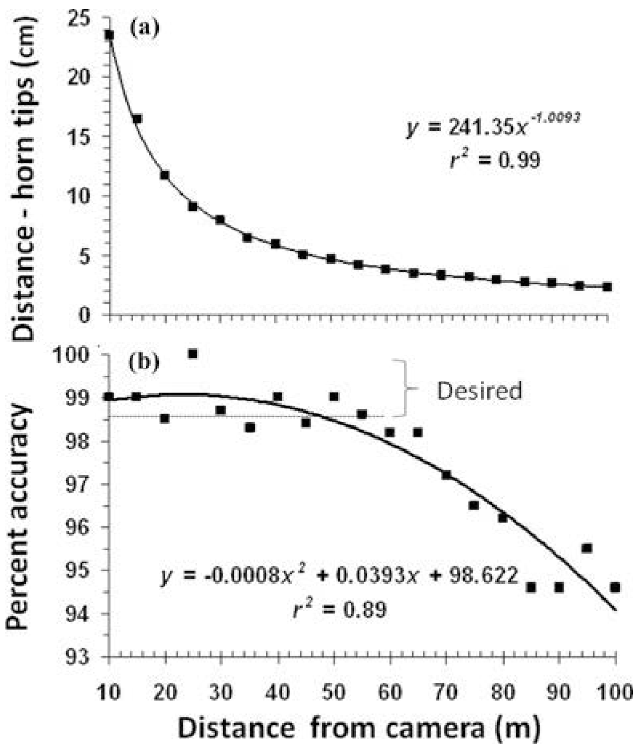


*Figure 3. (a) Relation between distance at which an animal was photographed and change in digital measure of a feature on that animal and (b) percent accuracy of the estimated size of a feature as a function of distance at which the photograph was taken. The feature measured (and its relative size reduction) is the distance between horn tips of a male muskoxen skull from Greenland.*

I took photographs of wild muskoxen from 2008 through 2010 in the Cape Thompson region, Alaska (U.S.A.), which includes Cape Krusenstern National Monument, and in and adjacent to Bering Land Bridge National Preserve on the Seward Peninsula, Alaska. These regions are the approximate western limits of wild muskoxen in North America (Lent 1999). The size of the former population was relatively stable and the latter was growing rapidly. Respective population sizes were ~ 350 and 2700 (Paul 2009). In April in each of 3 years, I photographed about 75–100 1- to 3-year-olds. Photographic sessions were normally completed within 25 minutes, and mean photograph distance that resulted in usable estimates of head size was 37.5 m (SE 6.58) ($n = 173$, range 14–54).

Between 1995 and 2004, I used techniques similar to those described above to photograph juvenile moose (*Alces alces shiras*) (Fig. 3) in and around Grand Teton National Park and Bridger-Teton National Forest near Jackson Hole, Wyoming (U.S.A.), where longitudinal profiles of radio-collared females were established (Berger et al. 2001; Berger 2007*a*, 2007*b*). Although data on head size and body mass were generated for Alaskan moose (*A. a. gigas)* (Bowyer et al. 1999), there is no evidence that the relation between size and mass of juveniles differs among subspecies. Even if it differed, remote measures of size alone would remain unaffected (Fig. 2).

## Analyses

Birth synchrony during a 10-year study of moose was high; 90% of 157 moose births occurred within 9 days (Berger 2007*a*). Given this narrow range, I excluded birth date as a covariate. I estimated juvenile body masses photogrammetrically between 1 December and 15 April. For photographs taken in October or November, 1.1 kg/day was added (Addison et al. 1994) until 1 December to avoid the possible confounding effects of seasonal variation in weight and skeletal growth (Cederlund et al. 1991).

I approximated juvenile mortality as follows. First, death was assumed when a female known to have given birth (i.e., a known mother) lacked offspring in successive sightings. Just once over 10 years did a known mother that subsequently lost her offspring later associate with a juvenile during the winter of the presumed loss of her offspring. Second, I assumed that bodies of young found near mothers without young were theirs. Although >25 carcasses were found, <33% could be assigned to a particular mother, and, of these, size measures were available for 5.

I detected at least 21 different orphans and inferred the fates of 16 through repeated sightings and ground surveys. Of these, 15 died. Of the 15 that died, I derived head-size estimates from 8; the bodies of 4 were recovered. Mass was estimated for a total of 48 young, but 17 were omitted from analyses because their fates could not be determined. Hence, models included data on size and associated mass of young, but not of all young. To increase the sample on fates of juveniles, the field team and I searched areas where orphans were last sighted over several weeks and disproportionally sampled regions of lower snowfall because moose avoid deep snow when possible. These efforts resulted in detection of 4 juvenile mortalities. Sampling biases may exist because surviving orphans could have moved to areas with deeper snow or beyond our search area.

I used stepwise, backward logistic regression (SPSS 2007) to examine the effects of 3 covariates: winter severity (snow depth), mass of young (photogrammetrically derived), and effect of maternal presence on a binary response variable, fate of young (survive or die) ($n = 40$) (Stewart et al. 2005).

Although orphans may be less apt to locate important feeding areas or more likely to flee than juveniles with mothers (Markgren 1975), I could evaluate only the extent to which orphans were recipients of aggression. I concentrated on female–female aggression to evaluate whether motherless young were more likely to be displaced during winter. I measured the frequency of aggressive behavior (charges, piloerection of nape fur, and head-down and ear-back postures) toward young during 10-minute bouts when either orphaned young or young with their mothers occurred within an estimated 100 m of an adult female.

Rates of aggression toward calves were weighted by contrasting the mean number of interactions per bout between young that were orphaned and young that were not orphaned (i.e., calf categories). However, because up to 6 interactions per bout occurred, I also assigned either 1 or 0 interactions per bout with contingency analyses. This nonparametric approach is more conservative because a binary measure reduces inflation from multiple interactions in any single bout. I used $t$ tests to compare means and Fisher's exact test to compare frequencies of aggression toward young with and without mothers.

To evaluate the effect of the severity of winter on survival of young, I used data on snow depth in Grand Teton National Park at the Moran substation (2057 m, 43°50′30″N 110°30′28″W) (Natural Resources Conservation Service 2009). Data from 1930 through 2005 were collated, and relations among snow depth on the first of January, March, and April quantified between-month and annual variation. Long-term average March snow depth was 98.35 cm (SD 24.37), but during the study the mean for 3 successive years was 132.92 cm (12.00). For the other 7 years, mean snow depth was 91.07 cm (SD 8.85), an approximately 45% difference. Consequently, winters were classified as either severe (former) or normal (latter), and these differed statistically ($p < 0.001$; $t = -6.23$).

## Results

The relation between distance between horn tips in photographs and distance at which the photograph was taken was best explained by $Y = 241.35x^{-1.0093}$ ($r^2 = 0.99$) (Fig. 2) (photographs were resized, however, to enable more accurate measures of horn width). I established that a minimum measurement error was <2% (Fig. 3). Beyond 65 m, measurement error ($Y$) increased as distance to the subject ($x$) increased ($Y = 2.074x + 89.942$) ($r^2 = 0.83$; $p < 0.001$) (Fig. 2).

The full logistic-regression model for effects of the 3 covariates on survival of juvenile moose was Pr(fate = 1) = 1/1+e$^{-z}$ with $z = -8.838 + 0.012$(mass) + 2.648(orphan status) + 1.292(winter type) ($\chi_3^2 = 9.58, p < 0.02$) (Fig. 4). Juvenile body mass and overwinter survival were not significantly related ($\chi^2 = 0.23$; $p = 0.63$). Maternal presence had a stronger effect on 1-year offspring survival ($p < 0.02$) than severity of winter ($p < 0.18$) (Table 1). Overall survival of calves without mothers was < 7 % (Fig. 4).

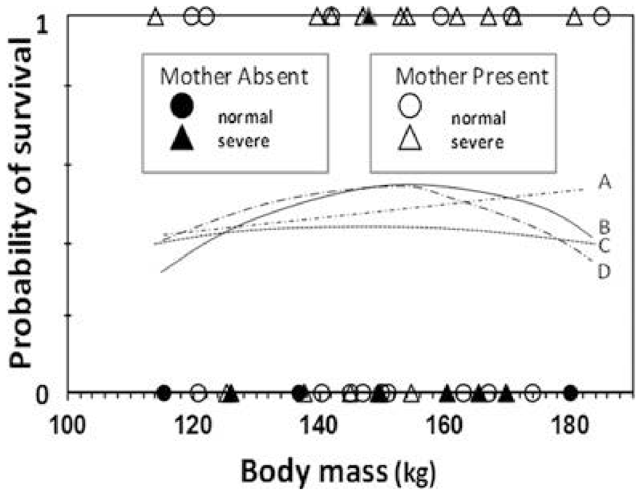


*Figure 4. Relation between survival of juveniles without mothers (mother absent) and of juveniles with mothers (mother present) as a function of winter severity (normal or severe) and estimated mass (described in text) in Jackson Hole, Wyoming (1995–2004). Letters show slopes for models (from Table 1): A, mass; B, full model; C, orphan; D, orphan and winter. Beta coefficients and SE for full model (respectively) are constant, −8.84, 4.50; mass, 0.01, 0.03; orphan, 2.65, 1.18; orphan-winter, 1.29, 0.74.*

Females without young on average displaced orphans 1.43 times/bout (SE 0.87), whereas young with mothers had little aggressive behavior aimed at them (0.03 times/bout [SE 0.37]; $t = 3.78$, $p < 0.0001$). Orphans were targets of aggression in 43% of the bouts ($n = 7$), whereas juveniles with mothers were targets in 5% of bouts ($n = 38$) ($p = 0.02$).

Head size of wild juvenile muskoxen did not differ between study areas (2-way analysis of variance, $F_{1,113} = 0.001, p = 0.97$), but differed among years ($F_{2,113} = 12.52$, $p < 0.001$) (Fig. 5). On average, reduction in head size was 17% (Bering Land Bridge) and 24% (Cape Thompson) in 2009 relative to the 2008 maximum ($p < 0.001$), and reduction in head size also differed between 2009 and 2010 ($p < 0.02$).

## Discussion

### Photogrammetry and Conservation Science

To be of value to conservation, the use of photogrammetry must provide statistically robust data, be practical to use across a wide range of situations, and yield results that can be used to address important questions. The first of these requirements is least subjective, given the variety of statistical approaches available to assess accuracy and precision. The species I examined—moose and

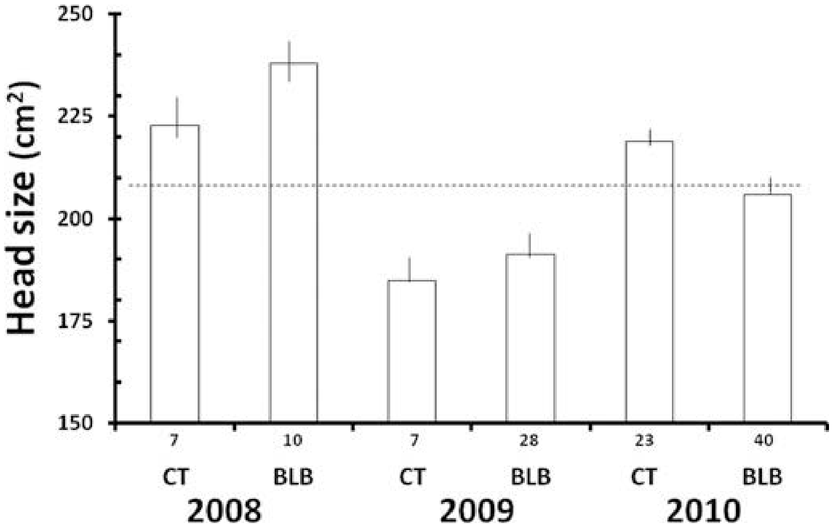


*Figure 5. Mean head size of 1-year-old muskoxen (n = 115; males and females combined) at Cape Thomson (CT) and Bering Land Bridge (BLB) (western Alaska) calculated from photographs (numbers along x-axis, sample size; error bars, standard error of the mean; dotted line, mean across all years).*

muskoxen—are relatively large-bodied and do not readily flee when approached. These factors allowed me to estimate the size of traits from photographs taken at distances of typically <40 m. The second requirement was satisfied because photogrammetry was not restricted to any given habitat, the necessary equipment was easily managed, and measuring features on the photographs was straightforward. Finally, although relevancy of data is somewhat subjective, in this case traits can be applied to an understanding of juvenile recruitment or annual variation.

Among long-lived mammals, population declines are generally characterized more by changes in juvenile than adult mortality (Gaillard et al. 2000). Factors that compromise the importance of surviving juveniles to population growth rate (lambda) are small size or poor condition, related factors that both delay puberty (Festa-Bianchet et al. 1997, 1998; Steinheim et al. 2002) and can exacerbate mortality (Adams & Dale 1998; Bowen et al. 2003). Given that smaller individuals may be less fecund than larger individuals (Loison et al. 1999; Keech et al. 2000; Solberg et al. 2004, 2008), remote assessments of size may help in the understanding of how resources and weather affect individual contributions to population processes. Poor-quality habitat, for example, restricts growth and affects the onset of puberty in such distantly related species as tuatara (*Sphenodon guntheri*), harbor seals (*Phoca vitulina*), and elephants (*Loxidonta africana*) (Hoare et al. 2006; Pistorius et al. 2008; Owens & Owens 2009).

**Table 1. Results of logistic regression of overwinter survival of juvenile moose as a function of the individual's estimated mass, winter severity (winter), and presence or absence of an individual's mother (orphan).[a]**

| *Model and term* | *Coefficient* | *z* | *p > \|z\|* | $\chi^2$ | *p>* | *Log likelihood* | *95% CI* |
|---|---|---|---|---|---|---|---|
| Full model | | | | 9.58 | 0.02 | −22.737 | |
| Mass | 0.012 | 0.55 | 0.58 | | | | −0.030 to 0.054 |
| Orphan | 2.648 | 2.25 | 0.03 | | | | 0.337 to 4.958 |
| Winter | 1.292 | 1.74 | 0.08 | | | | −0.163 to 2.747 |
| Constant | −8.838 | −1.97 | 0.05 | | | | −17.650 to −0.026 |
| Orphan status × winter | | | | 9.27 | 0.01 | −22.891 | |
| Orphan | 2.610 | 2.23 | 0.03 | | | | 0.319 to 4.900 |
| Winter | 1.271 | 1.73 | 0.08 | | | | −0.170 to 2.713 |
| Constant | −6.934 | −2.55 | 0.01 | | | | −12.266 to −1.601 |
| Orphan status | | | | 6.09 | 0.01 | −24.481 | |
| Orphan | 2.274 | 2.03 | 0.04 | | | | 0 .078 to 4.470 |
| Constant | −4.353 | −2.02 | 0.04 | | | | −8.570 to −0.136 |
| Mass | | | | 0.23 | 0.63 | −27.409 | |
| Mass | 0.001 | 0.48 | 0.63 | | | | −0.028 to 0.045 |
| Constant | −1.528 | −0.55 | 0.58 | | | | −6.992 to 3.936 |
| Winter | | | | 1.82 | 0.18 | −26.615 | |
| Winter | 0.875 | 1.33 | 0.18 | | | | −0.415 to 2.166 |
| Constant | −1.569 | −1.44 | 0.15 | | | | −3.701 to 0.563 |

*[a]Data collected 1995–2004 in and adjacent to Grand Teton National Park, Wyoming (U.S.A.).*

### Photogrammetry and Conservation Policy

Public agencies are charged with managing quotas for harvested species. At different times and in different places, the shooting of female moose with young has been permitted under the assumption that calf survival is minimally affected. Although researchers in Scandinavia have concentrated on how the amount of snow and presence of mothers affect juvenile survival (Markgren 1975; Cederlund et al. 1991), the role of juvenile size on survival is not especially clear (Solberg et al. 2004, 2008). My results (Fig. 4) indicate that a social factor (maternal absence) and not juvenile size is strongly associated with mortality and its effects are exacerbated during severe winters. Orphans were subjected to 8–47 times more aggression than juveniles with mothers. Whether such aggression intensifies winter mortality is uncertain, but in the absence of mothers, juveniles likely incur greater metabolic costs and expend more energy in deep snow than juveniles with mothers. Wyoming's Game and Fish Department used such information (in the late 1990s) as a basis for disallowing harvest of adult females with calves.

Noninvasive photographic measures of phenotypic traits have been applied in other ways. Estimates of horn sizes and their regrowth in black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceroses (which are poached for their horns) contributed to decisions about horn removal as a conservation strategy (Berger et al. 1993; Rachlow & Berger 1998). Use of estimates of horn size derived from photographs cost less and was less dangerous to animals than repeated immobilization. Monitoring of the sizes of horns or antlers (Bergeron 2007) with photogrammetry may also help achieve management goals, given interests in the harvest of animals with large antlers or horns.

### Advantages and Constraints of Photogrammetry

The advantages of photogrammetry are that it is noninvasive, increases sample sizes, requires equipment that is durable and relatively inexpensive, may be possible to use in monitoring programs, and has a case-specific potential to inform conservation. The technique also has constraints; it may lack accuracy and may be applicable only to juveniles. Photogrammetry has been used to estimate the size of marine mammals, primates, and ungulates, but the technique has been most effective at relatively short distances (Bell et al. 1997; Bergeron 2007). When used to estimate the sizes of seals and monkeys, the distance at which photographs were taken was restricted to <20 m (McFadden et al. 2006; Rothman et al 2008).

Although estimates of head size derived from photographs have been used to estimate mass in bison, muskoxen, and moose, head size and mass are related only in prepubescent individuals. Presumably, this is because young animals invest somatically in skeletal growth. Among adults, increased variance in mass or a lack of a relation between size and mass is likely due to varied body condition that results from past or current reproduction (Berger & Cunningham 1994; Festa-Bianchet et al. 1998).

Additional constraints of photogrammetry are related to interpretation, ecological complexity, and practicality. For instance, although photographs can be used to estimate size, identification of ecological sources of observed variation will always require more information. And, there are other practical issues. For non-habituated or hunted species and populations, the proximity required for photographic accuracy may become unattainable. Parallel lasers are useful for size estimation under some conditions (Durban & Parsons 2006), but laser performance is affected by wind, precipitation, and object shape and structure. In addition to the size of the subject being photographed, light conditions affect photographic accuracy. Nocturnal and forest animals also are challenging to photograph because visibility at night is reduced and the animals can be of small size. Furthermore, human presence disturbs animals and may lead to site abandonment. When gathering data on animal mass is a goal, size-mass relations must be validated (Cattet & Obbard 2005). For head-size measurements, deviations from perpendicular (for lateral) or direct (frontal) shots decrease accuracy. Differences in one's ability to measure different animals may result in additional variation (Waite & Mellish 2009). Last, it may be dangerous to photograph large animals at close proximity.

Despite these caveats, photogrammetry avoids repeated handling of animals and minimizes the risk of mortality and the expense of capture. Size is affected by nutrition and hence may further understanding of how particular animal traits respond to environmental conditions, although maternal effects will play some role (Monteith et al. 2009). As my results suggest, size metrics may be sensitive to annual variation in weather and have potential to inform conservation policy.

## Acknowledgments

Grants from the National Science Foundation, National Geographic, National Park Service, U.S. Geological Service (Biological Resource Division), Wildlife Conservation Society, and Charles Engelhard Foundation helped fund this research. For other support, I thank Alaska Department of Fish and Game, National Park Service (Grand Teton and Western Arctic), Quicksilver Air, University of Montana, and Wyoming Department of Fish and Game. Field or technical support were provided by J. Bohne, S. Cain, E. Cheng, C. Cunningham, F. Goodhope Jr., G. Helfrich, M. Johnson, S. Kilpatrick, J. Lawler, K. Murray, J. Pomeroy, M. Reid, T. Roffe, G. Roffler, B. Shults, R. Seidler, E. Seigh, R. Schaeffer Jr., and J. Weinowama. P. Barboza arranged for use of the Large Animal Research

Center (University of Alaska). J. Ward Testa graciously arranged data on yearling moose. L. Adams, J. Brodie, R. Harris, C. Hartway, 3 anonymous reviewers, N. Horning, E. Fleishman, and E. Main improved prior drafts. I thank all.

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