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ARTICLE

Detecting between-individual differences in hind-foot length in populations of wild mammals

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Abstract: Hind-foot length is a widely used index of skeletal size in population ecology. The accuracy of hind-foot measurements, however, has not been estimated. We quantified measurement error in adult hind-foot length in yellow-bellied marmots (*Marmota flaviventris* (Audubon and Bachman, 1841)), mountain goats (*Oreamnos americanus* (de Blainville, 1816)), and bighorn sheep (*Ovis canadensis* Shaw, 1804) from long-term capture–recapture studies. Fitting a linear mixed effect model for each species separately, we found that hind-foot length was significantly repeatable in the three species, but repeatability was low, ranging from 0.30 to 0.47. Measurement error explained 53%–66% of the variance in foot length. Differences of 6, 13, and 27 mm would be indistinguishable from measurement error for marmots, goats, and sheep, respectively. At least 4–6 measures per individual were needed to detect variation in foot length between individuals of a population using a mixed effect model. Researchers should strive to limit measurement errors because inaccurate measures may obscure important biological patterns.

Key words: accuracy, repeatability, yellow-bellied marmot, mountain goat, bighorn sheep.

Résumé : La longueur du pied arrière est un indice de la taille du squelette couramment utilisé en écologie des populations. L'exactitude des mesures de pied arrière n'a toutefois jamais été estimée. Nous avons quantifié l'erreur de mesure de la longueur du pied arrière d'adultes pour la marmotte à ventre jaune (*Marmota flaviventris* (Audubon et Bachman, 1841)), la chèvre de montagne (*Oreamnos americanus* (de Blainville, 1816)) et le mouflon d'Amérique (*Ovis canadensis* Shaw, 1804) à partir de données d'études de capture–recapture de longue durée. En réalisant un modèle linéaire mixte pour chaque espèce, nous avons constaté que les mesures de la longueur du pied arrière étaient significativement répétables pour les trois espèces, mais que cette répétabilité était faible, allant de 0,30 à 0,47. L'erreur de mesure explique de 53 % à 66 % de la variance des mesures de longueur du pied. Il serait impossible de distinguer des différences de 6, 13 et 27 mm de l'erreur de mesure pour les marmottes, les chèvres et les mouflons, respectivement. Un minimum de quatre à six mesures par individu était nécessaire pour détecter les variations de la longueur du pied entre individus d'une même population en utilisant un modèle mixte. Les chercheurs devraient s'efforcer de limiter les erreurs de mesure puisque des mesures inexactes peuvent masquer des effets biologiques importants. [Traduit par la Rédaction]

Mots-clés : exactitude, répétabilité, marmotte à ventre jaune, chèvre de montagne, mouflon d'Amérique.

Introduction

In many species, body size is a key determinant of fitness (Stearns 1992; Gaillard et al. 2000; Roff 2002). Although numerous studies have shown the influence of body size on reproduction, survival, and population dynamics (for reviews see Blanckenhorn 2000 and Gaillard et al. 2000), few have addressed the accuracy of body-size measurements (Palmer 1994; McLaren and Curran 2001; Garel et al. 2010). The ability to identify important evolutionary patterns and factors shaping them depends on the accuracy and the precision of repeated measures. Measurement accuracy and precision also have important consequences for population monitoring, because more data are required when measurements are inaccurate and imprecise.

Body-size measurements of harvested mammals can have measuring errors of less than 2% (McLaren and Curran 2001; Garel et al. 2010). However, precision of body-size measurements declines for live individuals (8%–25% variation in repeated measurements; Garel et al. 2010). Field conditions and stressed animals often lower the precision of measurements on nonsedated subjects. Species size and morphology also create specific challenges to restraining individuals and measuring body-size traits accurately and precisely. Good trait measurements are especially important when individual variation has important evolutionary implications (Hayes and Jenkins 1997).

Skeletal measures have been used as an index of body size in several studies of growth, development, and population dynamics (Suttie and Mitchell 1983). Foot length is easy to measure on both live and dead animals and is widely used in both birds and mammals (Green 2001). Hind-foot length has been used to correct body mass by skeletal size to obtain a body condition index (Green 2001). For mammals, hind-foot length has also been related to population density and has been used as an index of individual phenotypic quality (McElligott et al. 2001; Toïgo et al. 2006; Zannèse et al. 2006; Couturier et al. 2010; Taillon et al. 2011). Despite the wide use of hind-foot length in ecology, the precision of its measurements has not been thoroughly examined (but see Garel et al. 2010).

Here, we quantify measurement error and assess the number of measurements needed to detect significant variation in hind-foot length between individuals in a wild population. Because in most

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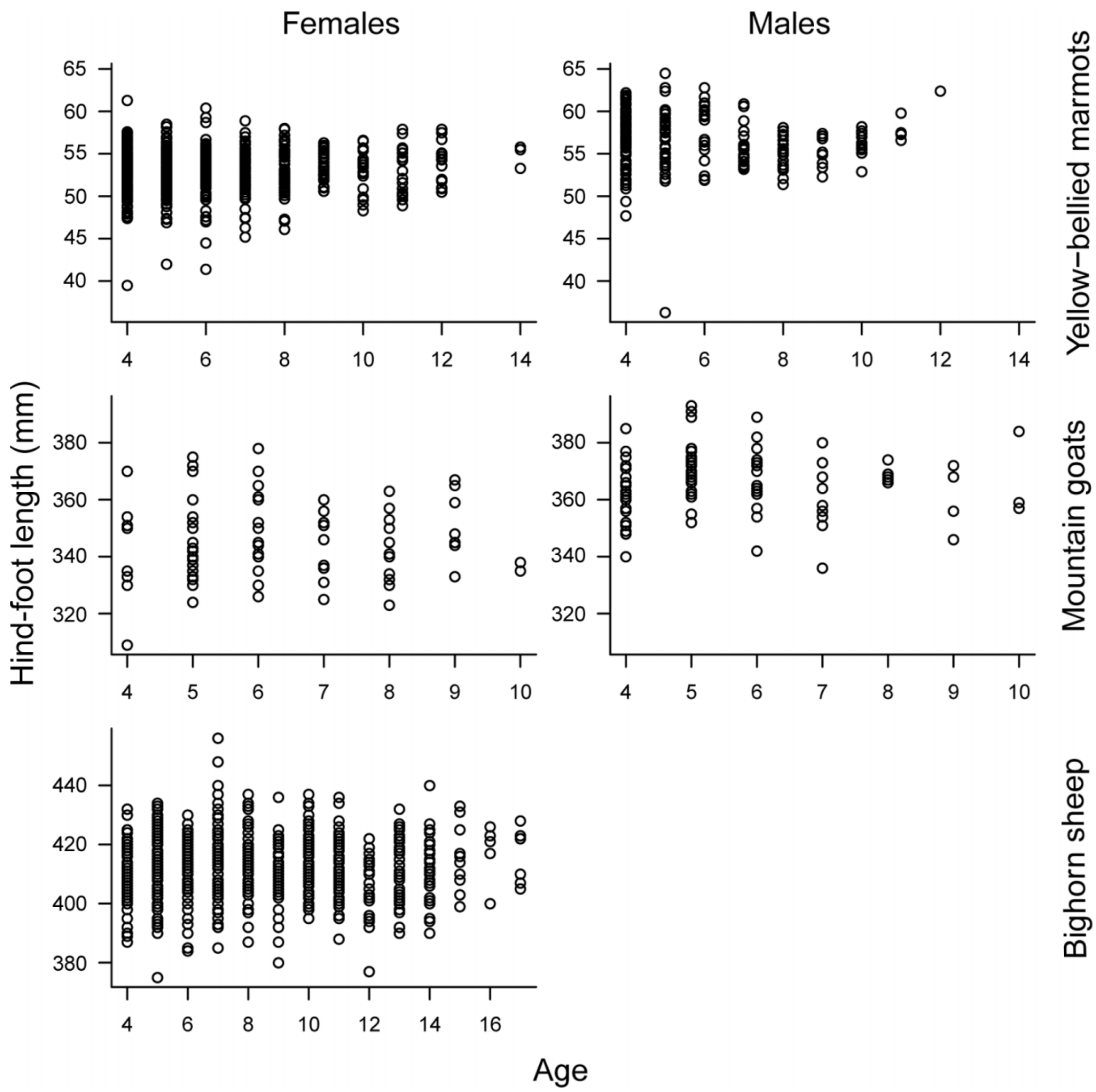
Fig. 1. Variation of hind-foot length with age for males and females in three free-ranging wild mammals (yellow-bellied marmots (*Marmota flaviventris*), mountain goats (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*)).



mammals, hind foot stops growing early in life and does not shrink during physiological stress (Klein 1964; Suttie and Mitchell 1983), we used repeated measures of adults over several years to assess measurement errors and between-individual variation. We used data from three long-term studies of wild mammals: yellow-bellied marmots (*Marmota flaviventris* (Audubon and Bachman, 1841)), mountain goats (*Oreamnos americanus* (de Blainville, 1816)), and bighorn sheep (*Ovis canadensis* Shaw, 1804). We had three goals. First, evaluate measurement error on hind-foot length. Second, estimate between-individual variation (i.e., repeatability) and determine if it was significant. Third, estimate how many measurements per individual were needed to detect between-individual variation in hind-foot length based on resampling of existing data.

Materials and methods

For the three species (marmots, goats, and sheep), hind-foot length is not expected to grow for animals 4 years or older (Fig. 1 and below). We thus used data for individuals 4 years or older with at least two measurements. Data were collected following a capture–recapture protocol. All animals were individually marked and of known age because they were first trapped as juveniles or yearlings (marmots: Ozgul et al. 2010; bighorn sheep: Festa-Bianchet et al. 1996; mountain goats: Côté et al. 1998). Animal care protocols following Canadian Council on Animal Care (CCAC) guidelines have been approved by University of California, Université Laval, and Université de Sherbrooke animal care committees for marmots, goats, and sheep, respectively.

Yellow-bellied marmots

From 2002 to 2011, marmots were trapped regularly during summer using Tomahawk live traps baited with oats and salt or horse-feed near the Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA (Armitage 1986). Trapped marmots were measured in a canvas handling bag. Left hind foot—the distance between the heel and the center front of the foot pad—was measured using an electronic caliper to the nearest 0.1 mm. Toes were not included because it was not possible to consistently extend them for measurement.

Mountain goats

Mountain goats were measured from 1988 to 2011 at Caw Ridge, Alberta, Canada (Côté et al. 1998). They were caught in Clover and

Table 1. Number of measurements and descriptive statistics of left hind-foot measures (mm) in three long-term studies of free-ranging wild mammals.

				Population level				Individual level		
Species	N_{obs}	N_{ind}	N_{year}	Mean	Range (width)	σ	CV	Mean Δ	Max Δ	σ
Yellow-bellied marmots (*Marmota flaviventris*)	946	97	8	53.7	36.3–64.5 (28.2)	2.9	5.5	5.2	23.6	2.0
Mountain goats (*Oreamnos americanus*)	94	40	22	356.3	309–393 (84)	16.4	4.6	12.5	35.0	7.9
Bighorn sheep (*Ovis canadensis*)	670	56	21	411.8	375–456 (81)	11.1	2.7	26.5	53.0	8.0

Note: Δ corresponds to the difference between longest and shortest measure for one individual. CV is the coefficient of variation.

Fig. 2. Individual mean (circles) and range (lines) of hind-foot measures in three free-ranging wild mammals (yellow-bellied marmots (*Marmota flaviventris*), mountain goats (*Oreamnos americanus*), bighorn sheep (*Ovis canadensis*)). Solid circle and solid lines represent females, whereas open circles and broken lines represent males. Foot length was standardized (centered and reduced) for each species to ease between-species comparison.

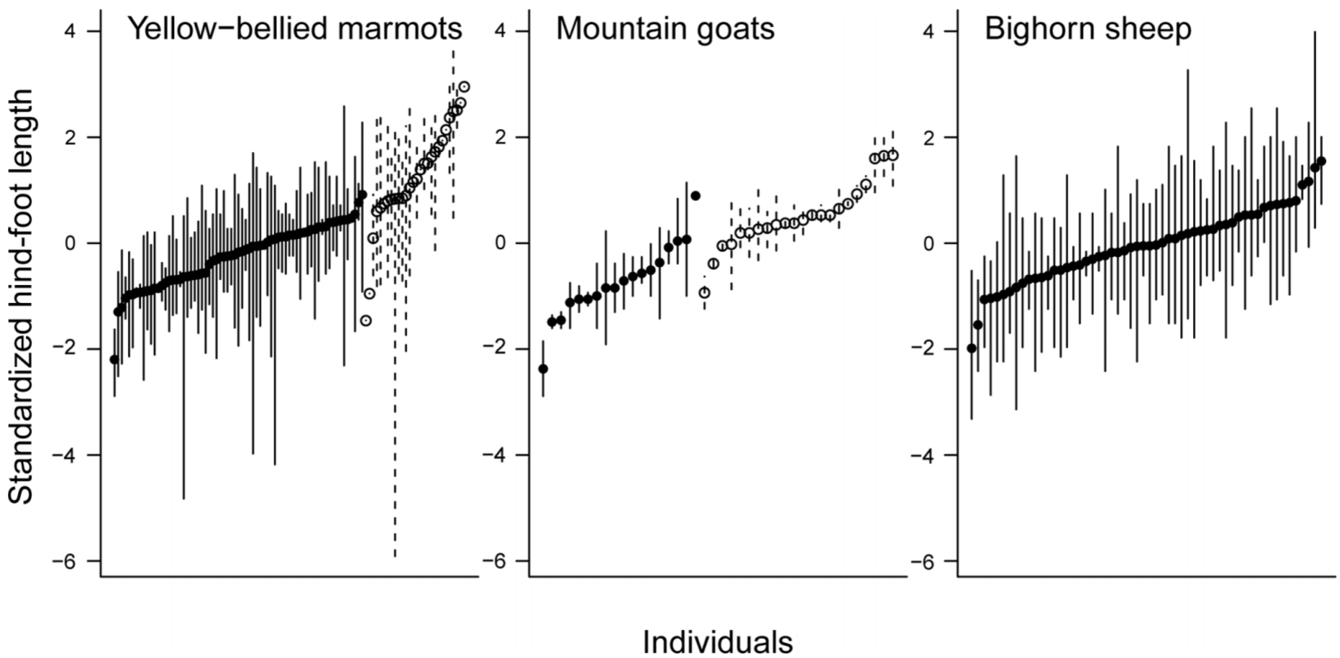


Table 2. Partitioning of variance in left hind-foot measures in three long-term studies of free-ranging wild mammals.

	Variance			Proportion of variance		
Species	Individual	Year	Residual	Individual	Year	Residual
Yellow-bellied marmots (*Marmota flaviventris*)	2.2	0.33	4.8	0.30	0.04	0.66
Mountain goats (*Oreamnos americanus*)	78.9	<0.001	90.3	0.47	<0.001	0.53
Bighorn sheep (*Ovis canadensis*)	54.2	7.1	68.8	0.42	0.05	0.53

Note: Measurement error variance is defined as the sum of residual and year variances.

Stephenson box traps baited with salt, and adults (≥3 years) were chemically immobilized with xylazine, whose effect was reversed by intramuscular injection of idazoxan (Haviernick et al. 1998). Animals were blindfolded and hog-tied (i.e., three legs tied together with a rope) during measurements. Left hind-foot length was measured using a soft tape from the calcaneum to the hoof tip. Mountain goat were normally trapped as yearlings, 2-year-olds, and once or twice after that during their adult life (Côté et al. 1998). Since 1994, at least 80% of captures and hind-foot measurements were done by the same person (S.D.C.).

Bighorn sheep

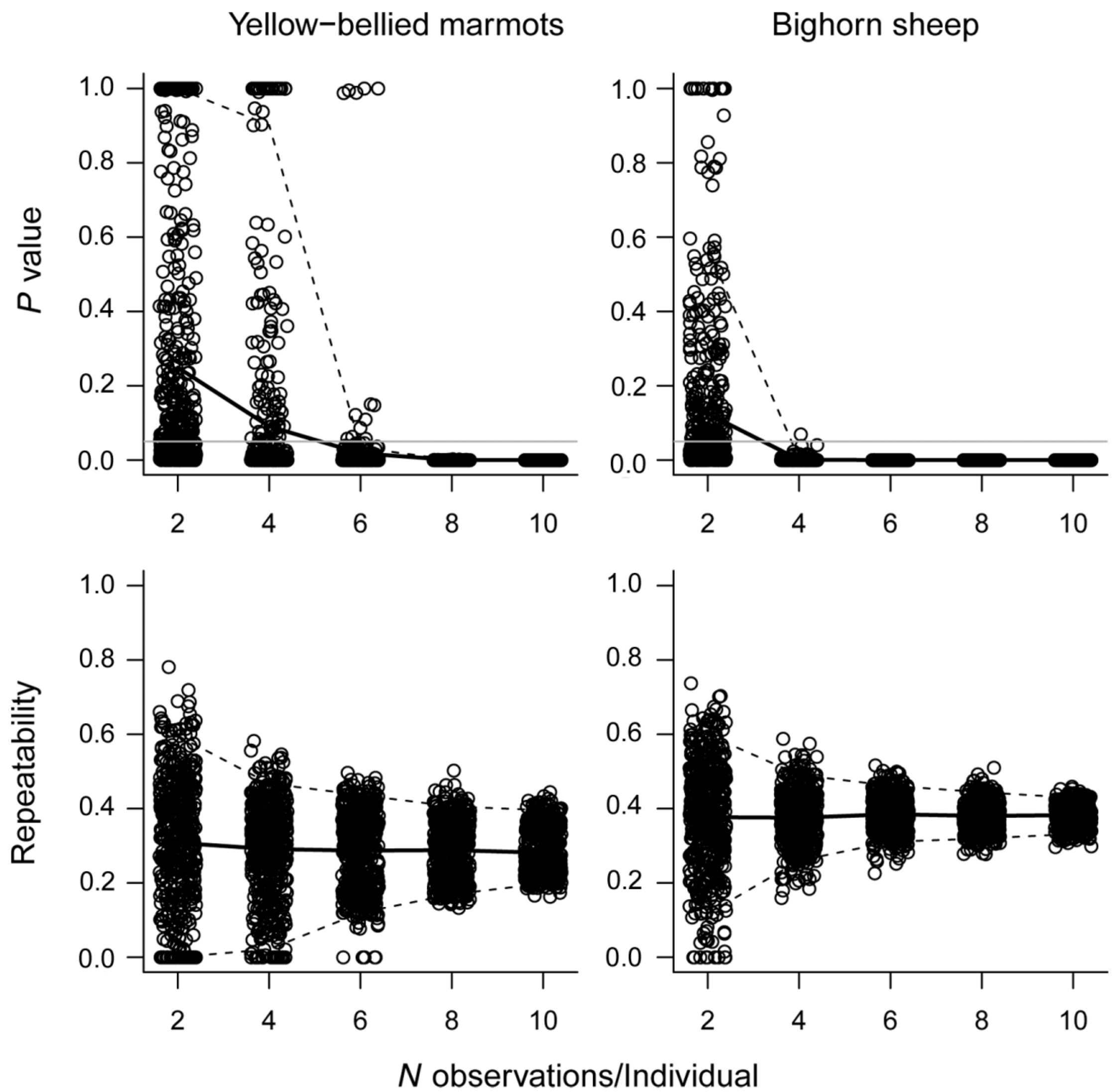
Bighorn sheep were measured at Ram Mountain, Alberta, Canada, from 1975 to 1992, after being caught in a corral trap baited with salt (Festa-Bianchet et al. 1996). Sheep were manually restrained, blindfolded, and hog-tied. Hind-foot length was measured with a soft tape from the calcaneum to the hoof tip.

Statistical analyses

Error and between individual variance

We first computed descriptive statistics (range, maximum difference, σ, coefficient of variation) of variation in hind-foot length at both population and individual levels for each species. To estimate measurement error and repeatability of hind-foot length, we fitted a linear mixed model for each species. We included sex as a fixed effect to control for sexual dimorphism. Since bighorn sheep data included only females, sex was not fitted for this species. Individual identity and year were fitted as random effects. Exact age of adults as a factor, either as a linear or as a quadratic effect, was not a significant covariate for any of the species (Fig. 1).

Fig. 3. Probability to detect individual differences and repeatability as a function of the number of measurements per individual when resampling yellow-bellied marmots (*Marmota flaviventris*) and bighorn sheep (*Ovis canadensis*) data. The horizontal grey line in the top two panels represents the 0.05 significant threshold. The thick black lines represent the mean, whereas the broken lines represent the 95% quantile of the *p*-value distribution and the 2.5 and 97.5 quantiles of the repeatability distribution.



Thus, if hind-foot length in adults was measured without error, all variation should be between individuals. Variance associated with the individual identity random effect represents interindividual variance. Because we did not know who took each measurement, we were unable to estimate intraobserver and interobserver variations. Observers changed nearly every year, as customary for long-term studies. For mountain goats, however, most measures were taken by the same person. The variance associated with year could be interpreted as the minimum interobserver variance. Measurement error variance was the sum of the year and residual variances. Significance of random effects was assessed using a log-likelihood ratio test (LRT) comparing models with and without the random effect and fitted using restricted maximum likelihood (REML; Pinheiro and Bates 2000).

Number of measurements required to study individual variation

For 33 bighorn sheep and 31 marmots with at least 10 measurements each, we randomly selected (without replacement) 2, 4, 6, 8, and 10 measurements for each individual. We did this by resampling 500 times for each number of measurements per individual. We then ran the same linear mixed model as previously described on each of the 2500 data sets created for each species. We estimated repeatability and significance of the interindividual variation for each model. We considered that the number of measurements per individual was sufficient when at least 95% of the models suggested significant individual variation. All analyses were ran in R version 2.14.0 (R Development Core Team 2011) using the lmer function in the lme4 package (Bates et al. 2011).

Results

We analyzed 1710 hind-foot measures from 193 individuals (Table 1). Coefficients of variations in foot length at both the population and individual levels were highest in marmots and lowest in bighorn sheep (Table 1, Fig. 2). The mean difference between the longest and shortest measures for the same individual was 5.2, 12.5, and 26.5 mm for marmots, goats, and sheep, respectively (Table 1). Measurement errors explained 53%–70% of the variation in hind-foot length (Table 2, Fig. 2).

Individual variation was significant in all species (marmots: $\chi^2_{[1]}$ = 135, $p < 0.001$; goats: $\chi^2_{[1]}$ = 13.2, $p < 0.001$; sheep: $\chi^2_{[1]}$ = 231,

$p < 0.001$) with repeatability of 30%–47% (Table 2). Year was significant in marmots and sheep (marmots: $\chi^2_{[1]} = 27.7$, $p < 0.001$; sheep: $\chi^2_{[1]} = 29.7$, $p < 0.001$), explaining 4% and 5% of the variance, respectively (Table 2). Year was not significant for goats ($\chi^2_{[1]} < 0.001$, $p > 0.99$) (Table 2).

At least six measures for marmots and four measures for bighorn sheep were needed to detect individual variation in at least 95% of the simulations (Fig. 3). Repeatability could be highly under- or over-estimated (range: 0–0.8) when using fewer than 6 and 4 repeated measurements per individual for marmots and sheep, respectively (Fig. 3).

Discussion

We found significant between-individual differences (i.e., repeatability) of hind-foot length in the three species we studied. Measurement error, however, accounted for up to 70% of variation in hind-foot length. The variance associated with measurement error was much higher than reported in roe deer (*Capreolus capreolus* (L., 1758)), i.e., 25% and 8% in two populations (Garel et al. 2010), or in birds (20%; Perktaş and Gosler 2010). The difference in measurement error between birds and mammals could be explained by different morphology. In birds, the tarsometatarsal bone is clearly identifiable when bending the foot articulation (Bairlein 1995). Hind-foot length in mammals includes multiple bones (tarsal, metatarsal, and phalanges) and articulations that must be straightened for accurate measurement. Tools to increase accuracy and precision of measurements such as the guttered caliper used on roe deer (Garel et al. 2010) are necessary to decrease measurement error and increase consistency.

Year explained 5% or less of the variance in hind-foot length, indicating that variation due to observers was not substantial. Absence of a year effect in mountain goats demonstrated the value of having a limited number of persons taking measurements over the years, although the relatively small data set used for goats might have decreased the power to detect year-to-year variation. Despite only one highly trained person taking more than 80% of measurements on mountain goats for the last 18 years, the error variance was 53%, indicating the need for tools to minimize error.

Chemical immobilization of mammals is sometimes necessary for safety reasons for both animals and staff (West et al. 2008). However, chemical immobilization could have physiological and life-history consequences (Côté et al. 1998; Pelletier et al. 2004; Fahlman et al. 2011). Our results suggest that chemical immobilization does not increase precision of measurements: the proportion of measurement error was similar in mountain goats and bighorn sheep despite the fact that mountain goats were drugged but sheep were not.

At least 4–6 measurements per individual were needed to detect between-individual differences. This is not a problem for long-term studies with a high recapture rate. For the marmot and sheep studies, yearly recapture rate was higher than 95%. For mountain goats, however, fewer repeated measurements were available because of the risk of repeated captures (Côté et al. 1998). It should be noted that the estimate of 4–6 measurements is based on adult (nongrowing) individuals. Growing individuals would need more frequent measures to separate measurement error from growth.

Our results also showed that differences in hind-foot length smaller than 6, 13, and 27 mm would be indistinguishable from measurement error for marmots, goats, and sheep, respectively. With such large errors, many topics such as asymmetry and growth may be difficult to study accurately. Possible ways to decrease measurement errors include limiting the number of observers, increasing their training to better standardize measurements, and developing more accurate tools. A guttered caliper could work well for ungulates (Garel et al. 2010); however, it could not be used when animals are hog-tied. Hog-tying animals increases safety for both handlers and animals. For rodents, a transparent hard plexiglass ruler with a right angle to position the heel might be useful to consistently extend the foot, and thus increase accuracy and precision of measurements. When the individual is on its back, the hind foot could be pressed on the ruler with the heel blocked by the right angle; foot length could then be read through the ruler.

Hind-foot length has many advantages compare with other body-size measurements. It is relatively easy to measure without harm within a capture–release protocol (Suttie and Mitchell 1983) and is related to population density in juveniles (roe deer: Zannèse et al. 2006) and yearlings (caribou (*Rangifer tarandus* (L., 1758)): Pachkowski 2012). Thus, hind-foot length is an excellent measure for long-term population monitoring for management and conservation. Hind-foot length could also be used as a skeletal size measure in adults, as it stops growing relatively early in life and does not shrink with stress or age. Minimizing measurement error of hind-foot length should be an important goal to increase our ability to study body-size variation in multiple species.

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