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FOOT LOADINGS AND PAD AND TRACK WIDTHS OF YELLOWSTONE GRIZZLY BEARS

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ABSTRACT.—I used measurements of grizzly bears (*Ursus arctos horribilis*) from the Yellowstone region, USA, to investigate relationships between widths of foot pads and widths of tracks, foot loading and pad size, incidence of tracks and type of activity, and widths of front-foot pads and gender and age-class. Track width was affected by substrates and increased relative to pad width as sizes of both pads and tracks increased. Foot loading (kg · cm^{-2}) did not vary substantially with foot size and so did not explain the proportionately larger tracks of larger animals. Tracks were most commonly associated with feeding activity that entailed excavation of fossorial foods (roots and rodents); they were least common when bears were feeding in the forest, feeding on ungulates, or traveling. Adult males and females could be differentiated by the width of their front-foot pads. Virtually all pads >14.5 cm wide belonged to adult or large subadult males. The pads of subadult females were most commonly <12.5 cm wide, whereas those of adult females were most commonly 12.5–14.5 cm wide.

Key words: grizzly bears, Ursus arctos, *pad width, track, age-class, gender, feeding activity.*

Compared to the tracks of ungulates and small mammals, bears tracks are of sufficient size and complexity to potentially allow for inferences regarding the identity of the associated animal (Edwards and Green 1959, Klein 1959). This potential is enhanced by the substantial size dimorphism between genders (Blanchard 1987). There is reason to expect that young bears could be differentiated from old bears, and adult females from adult males, on the basis of track size (Blanchard 1987). Many scientific studies and related management decisions categorize bear populations as subadult (weaned but pre-reproductive) and adult (reproductive) males and females. Because management situations can involve bears of unknown identity and because marking bears for research is difficult and expensive, there is potential value in being able to probabilistically ascribe gender and age-class to animals on the basis of their tracks (Reinhart and Mattson 1990).

Prior to the use of radio-telemetry, tracks were more commonly used to study large mammals. Edwards and Green (1959), Klein (1959), Valkenburg (1976), Pulliainen (1983), and Kendall et al. (1992) used bear tracks to estimate population trend or to identify individuals for estimating minimum population size. Identification of individuals from their tracks for these purposes is problematic (Edwards and Green 1959, Klein 1959). However, a probabilistic classification to gender and age-class is less so. Few researchers have attempted this less daunting task. Reinhart and Mattson (1990) classified bear tracks by gender and age, but without reference to a rigorous investigation of the sizes of bear feet and related sizes of tracks. Brooks et al. (1998) and Beck (1991) investigated relationships between foot sizes and gender and age-class for black bears (*Ursus americanus*), but without explicit reference to track sizes or bear activity.

In this paper I use foot measurements from grizzly bears (*Ursus arctos horribilis*) captured between 1975 and 1992 and field observations of a subset of these bears between 1986 and 1992 in the Yellowstone region of Wyoming, Montana, and Idaho, USA, to investigate relationships between (1) pad width and width of associated tracks at telemetry locations of radio-marked animals, (2) loading on foot pads and foot size, (3) type of activity by a bear and the likelihood that it left a measurable front-foot track, and (4) gender and age-class and width of the front-foot pad.

METHODS

Grizzly bears captured for research and management purposes were measured with a

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steel tape along 11 dimensions including the widest and longest parts of the front- and rear-foot pads (Fig. 1a; Blanchard 1987, M. Haroldson personal communication). Pad area was calculated as pad width times pad length times the proportion of this rectangle filled by the pad. Proportions for front and rear pads (0.67 and 0.70, respectively) were estimated from the generalized pad outlines and associated rectangles in Figure 1a. Bears were weighed using spring scales during 218 captures of 126 different bears. Only spring scale weights were used in this analysis. Bears were sexed and 95% were aged by counting the cementum annuli of an extracted first upper premolar (Mundy and Fuller 1964). Where this was not done, field crews subjectively classified the animal as subadult or adult based on body proportions, genital development, and evidence of reproduction. Subadults were defined as weaned animals <5 years old, unless the animal was a female accompanied by cubs. Precocious females such as these were classified as adults, which otherwise were animals ≥5 years old (Pease and Mattson 1999).

Of 203 captured bears, 172 were radiomarked and tracked by aerial telemetry for >1 month. The gender, age-class, and reproductive status were thus known for each marked bear during field observations for each year. Between 1986 and 1992, field crews visited 1027 telemetry locations, usually within 2 weeks of obtaining the location. At each location, tracks were measured when present and the bear's activity was classified based on observed sign (Mattson 1997, 2000). Several dimensions of front and rear tracks were measured, although track widths were emphasized for this analysis. Measurable front tracks were more commonly found than measurable rear tracks, presumably because of greater loading on front feet and their use in foraging, particularly in loose soil from excavations. Lengths of front-foot pads and tracks were not analyzed because of their greater variability compared to widths of both (Valkenburg 1976, Blanchard 1987). Most track widths were measured at the cusp of the upward curvature from the track base (Fig. 1b; Halfpenny 2000). However, the involvement of numerous field personnel in track measurements led to inconsistent application of this protocol, including the more vagarious measurement of track width

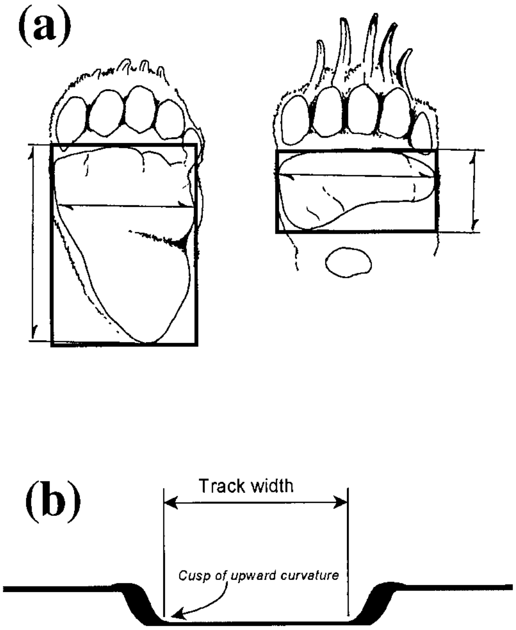

Fig. 1. (a) Front- and rear-pad measurements obtained from captured Yellowstone grizzly bears as indicated by arrows and brackets. Rectangles are the areas associated with the product of pad lengths and widths. The stylized rear and front pads make up approximately 70% and 67%, respectively, of the corresponding rectangles. (b) Idealized cross section of a front track showing the cusp of upward curvature and the location of track width measurements.

from rim to rim. Track substrates were described as snow, mud, or moist soil.

I used regression-type analyses to describe relationships between pad width and track width, pad width and bear age-class and gender, and pad surface area and bear weight. For the correlation between track and pad widths, I used analysis of covariance to control for the effect of substrate by entering it as a 2-category class variable (moist soil versus mud or snow). I combined mud and snow because initial models showed little difference in the effects of these 2 substrates on track measurements. Although there were errors in measurement of both pad and track widths, I used type I regression to describe the relationship between these 2 variables because of my interest in predicting pad width from track width (Sokal and Rohlf 1981). I used 3-term power equations ($y = b_0 + b_1x^{b_2}$) to describe relations between bear weights and pad surface areas, with the intent of estimating deviation of the power parameter (b_2)—and thus foot loading as a function of size—from 1.0. I treated individual bears as units of observation for this analysis and averaged weights and pad measurements for bears captured and measured multiple times. Bears measured as both subadults and adults were differentiated by age class.

I used logistic regression to describe relationships between the logit-transformed probability that an animal was of a given bear class and the width of its front-foot pad. Multiple measurements of an individual within a given age-class were also averaged and treated as a single observation for this analysis. I used polynomials and other transformations of pad width to maximize goodness-of-fit (Demaris 1992). Models were chosen so as to minimize the sample-size-corrected Akaike Information Criterion (AIC_c; Burnham and Anderson 1998). I also used AIC_c to specify a log-linear model relating track presence to type of bear activity. G^2 tests and R^2_L were used to describe goodness-of-fit and predictive efficiency (Demaris 1992). Because sampling of bears was nonrandom, probabilities of type I errors (*P*-values) are given only for comparison.

To calculate proportions by pad categories, I used weighted observations in the logistic regressions. Weighting factors were calculated by dividing the proportion of each gender and age-class in the sample of captured bears into the proportion of each class estimated to comprise the Yellowstone grizzly bear population during the time of this study (Pease and Mattson 1999). Proportions for subadult females, subadult males, adult females, and adult males in the population at large and for the sample of captured bears were 0.31, 0.20, 0.38, 0.11 and 0.17, 0.27, 0.31, 0.25, respectively. Thus, weighting factors were 1.78, 0.75, 1.22, and 0.44 for the 4 respective classes. Application of these weights did not inflate degrees of freedom, as the sum of weighted observations equaled the original sample size (218). Because the weights corrected for known bias in probabilities of sampling different classes, they are directly analogous to ratios applied to correct for bias in survey samples when strata are sampled with different known intensities (Williams 1978, Lehtonen and Pahkinen 1995). Resulting probabilities are thus applicable to field situations.

RESULTS

Widths of tracks were measured at 54 sites where known radio-marked bears had been located by telemetry. The strength of the relationship between pad and track widths from this sample was moderate when the effect of substrate was included (Fig. 2; $R^2 = 0.43$). The slope of the relation deviated from 1.0 ([1] and [2]; $n = 54$, $F = 19.5$, df = 2/51, $P < 0.0001$), with track widths increasing relative to pad widths as size of both increased (Fig. 2). I subsumed the effect of substrate into intercept terms and derived the following 2 substrate-specific equations from the general analysis-of-covariance model:

[1] Pad (cm) = 8.53 + 0.028 × (track [cm])^2 if substrate was moist soil.

[2] Pad (cm) = 7.29 + 0.028 × (track [cm])^2 if substrate was mud or snow.

Ground loadings of single front pads alone averaged 1.68 ($\pm 1s_{\bar{x}} = 2.34$) kg · cm^{-2} and of pairs of front and rear pads together averaged 0.45 (± 0.71) kg · cm^{-2}, assuming full weight of the animal was borne by the pad(s) in each case. The power parameter of the relation between scale weight and pad surface area did not substantially differ from 1.0 for either front-pad area alone (1.08 ± 0.28) or front- and rear-pad area combined (1.12 ± 0.22; Fig. 3). Thus, foot loading did not substantially increase with bear size.

The probability of finding a measurable track at a telemetry location of a radio-marked bear varied depending on the type of activity in which the bear was engaged (Fig. 4). Probabilities were greatest and exceeded 0.1 when an animal was engaged in excavating fossorial foods—roots and rodents. Probabilities were lowest when a bear was feeding in forests (for whitebark pine [*Pinus albicaulis*] seeds or ants from logs), traveling, or feeding on ungulate tissue. Probabilities were intermediate when animals were grazing or had excavated a daybed.

Sample sizes for activities not depicted in Figure 4 were too small ($n < 25$) to allow for confident estimation of probabilities. However, among the more sparsely sampled behaviors, fishing for cutthroat trout (*Oncorhynchus*

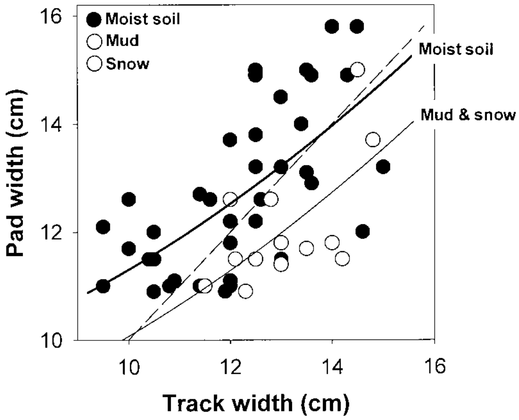

Fig. 2. Relationship between track width and pad width of feet of Yellowstone grizzly bears, 1986–1992. Solid lines describe the statistical relation between track and pad width for moist soil and mud and snow; the dashed line describes a 1:1 relation between the two. Solid circles denote measurements obtained from moist soil, gray circles measurements from mud, and open circles measurements from snow.

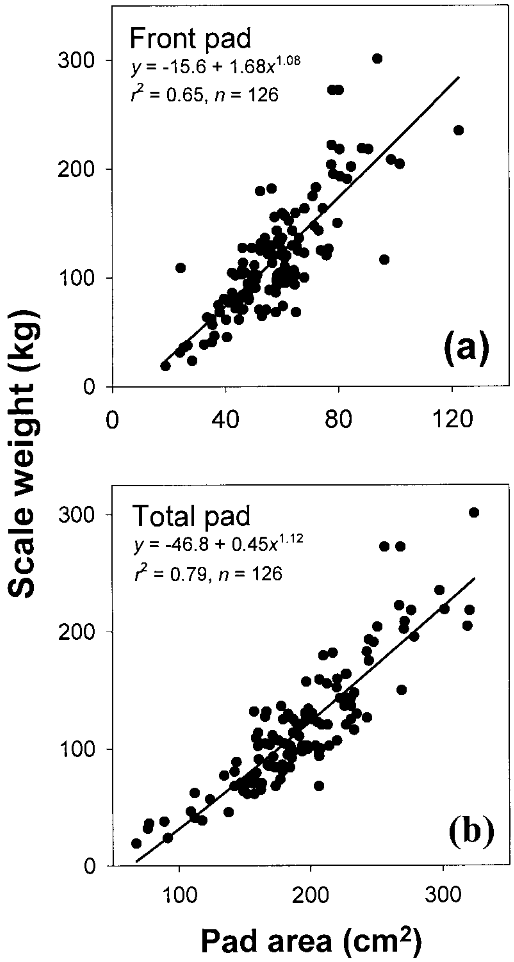

Fig. 3. Relationships between scale weight and (a) front-pad surface area and (b) total surface area of front and rear pads, for Yellowstone grizzly bears, 1975–1992. Lines represent the best fit of power functions ($y = b_0 + b_1 x^{b_2}$).

clarki) was unique because measurable tracks were found on 2 of 4 occasions that sign of fishing for cutthroat trout by marked bears was observed, 1986–1992. Few or no measurable tracks were found while bears were feeding on mushrooms, army cutworm moths (*Euxoa auxiliaris*), fleshy fruits, or ants from dirt and debris hills.

Informative relationships were evident between probabilities of gender and age-class membership and front-pad width for all classes except subadult males (Fig. 5; Table 1). Relations were strongest for adult females and adult males. The probability that a pad measurement was that of an adult female peaked between 12.5 and 14.5 cm, while the probability of the same for adult males escalated dramatically for measurements >14.5 cm. Pad widths overlapped considerably between adult females and subadult males. However, adult females were potentially additionally distinguished by the tracks of accompanying young. Measurable tracks of young were found on 1 of 6, 4 of 11, and 1 of 7 occasions when an adult female was known to be accompanied by cubs-of-the-year, yearlings, and 2-year-olds, respectively; i.e., tracks of yearlings were more likely detected than tracks of cubs or 2-year-olds.

Given these relationships, 12.5 and 14.5 cm provided useful cutoff points for pad-size categories. Large males, whether adult or subadult, constituted over 90% of all animals with pad widths >14.5 cm in size (Table 2). This category of large pads could therefore be considered roughly synonymous with reproductive or near-reproductive males. The 2 categories of smaller pad sizes were of mixed gender and age-classes, but with subadult females most prevalent in the ≤12.5 cm category and adult females most prevalent in the 12.5–14.5 cm category. Females of all ages accounted for over 80% of animals with pads ≤12.5 cm wide.

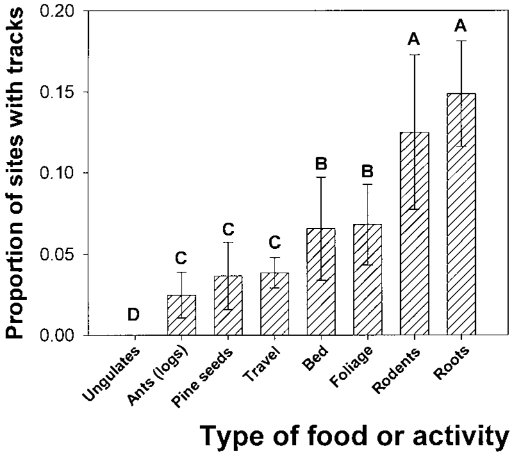

Fig. 4. Proportion of telemetry locations (±1 $s_{\bar{x}}$) visited by ground crews where measurable tracks of Yellowstone grizzly bears were found, by type of activity, 1986–1992. Activities denoted by the same letter (**A**–**D**) were combined in the best model describing the relation between probability of finding a measurable track and type of activity. Only types with $n \geq 25$ are shown.

Discussion

The variability in the correlation between track widths measured at telemetry locations of radio-marked bears and pads widths of the same bears probably arose for several reasons. As suggested by the analysis, tracks of the same bear will vary in size depending on the substrate. Differences in methods of measuring tracks (from inside cusp to inside cusp versus from outside rim to outside rim, as indicated in Methods) also will introduce variation (Halfpenny 2000). In fact, this difference in method was known to contaminate the track data collected during this study, although to an unknown degree. Perhaps most important, error in ascribing a measured track to a radio-marked bear could cause considerable variability in the relation between track widths and pad widths. This error would arise from failure of the assumption that all tracks measured at a telemetry location of a marked bear were of that bear alone. Such an assumption may not hold given that subadult siblings and consorting adults sometimes accompany each other and that other bears can be active within the spatial extent of the telemetry location error and the temporal extent of the sampling.

Even with the variable relation between track and pad widths, track measurements can provide information regarding the identity of the animal responsible for the track. Applications of this information would not be affected by errors relating a track to an individual animal if the interest is in gender and age-class alone. Furthermore, variance due to measurement method should be reduced if tracks are measured from inside cusp to inside cusp, as

TABLE 1. Features of logistic regression models ($y = b_0 + b_1 x_1 + b_2 x_2$ ...) describing relations between the logit-transformed probability of an animal being in 1 of 4 gender and age-classes and the width of its front-foot pad (cm), for Yellowstone grizzly bears, 1975–1992. The G^2 and P-values are for goodness-of-fit tests; larger values of the first and smaller values of the second indicate poorer fit. Superscripts of the independent variable *width* in the body of the table denote the power to which the variable is raised.

	Gender and age-class			
Model feature	Subadult female	Subadult male	Adult female	Adult male
First independent variable (x_1)	width^4	—	width^3	width^4
Second independent variable (x_2)	—	—	width^4	—
Third independent variable (x_3)	—	—	width^5	—
b_0 ($s_{\bar{x}}$)	1.22 (0.41)	−1.39 (0.17)	2.72 (2.35)	−7.74 (1.15)
b_1 ($s_{\bar{x}}$)	−0.00009 (0.00002)	—	−0.044 (0.016)	0.00017 (0.00003)
b_2 ($s_{\bar{x}}$)	—	—	0.0064 (0.0020)	—
b_3 ($s_{\bar{x}}$)	—	—	−0.00023 (0.00007)	
R_L^2	0.26	0.28	0.12	0.73
G^2	92	—	75	35
P	0.26	—	0.70	1.00
df	84	—	82	84
n	218	218	218	218

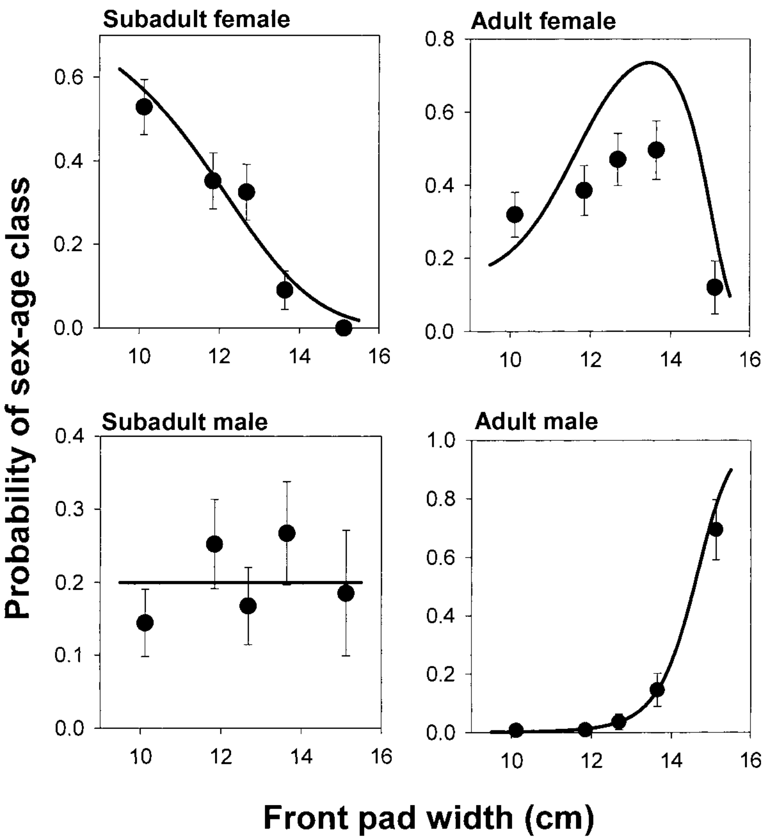

Fig. 5. Relationships between the probability that a front pad measurement was that of a given gender and age-class (subadult female, subadult male, adult female, and adult male) and width of the front pad, for Yellowstone grizzly bears, 1975–1992. Data points and associated standard errors are for measurements summarized by quintiles and are shown to illustrate goodness-of-fit.

recommended by Halfpenny (2000). The remaining cautionary point relates to the tendency for track width to proportionally increase relative to pad width as sizes of both increase. The relationship calculated between track and pad widths presented here could be used to correct for this tendency, assuming that there are no other uncorrected systematic biases. Without such a correction, bear classes strongly associated with larger tracks (i.e., adult males) could be overestimated relative to bear classes associated with smaller tracks.

The tendency for track widths to be proportionately larger than pad widths as size of both increased is not readily explained. Foot loading did not increase substantially with body size. Thus, I would not expect large bears to sink deeper than small bears in a given substrate and create proportionately larger tracks. Surface friction also would be comparable among bears of different sizes, and so I would not expect larger bears to create proportionately larger tracks because of greater lateral displacement. However, the predictably greater limb velocity of larger bears could cause both proportionately greater sinking and slippage. Also, this trend could be due to some unknown size-related bias in track measurement or ascribing tracks to marked bears.

Tracks promise to be useful for distinguishing small females and adult or large subadult males from all other classes. During this study, >90% of all front-foot pads wider than 14.5 cm were of adult or older subadult males while >80% of all pads narrower than 12.5 cm were of females. Of adult females with pads 12.5–14.5 cm wide, about one-quarter were identifiable by the presence of tracks from

TABLE 2. Proportions of genders and age-classes of Yellowstone grizzly bears in each of 4 pad-width categories. Proportions are weighted to account for discrepancies of genders and age-classes between captured bears and the population at large. Data were collected during 1975–1992.

Pad-width category (cm)	Gender and age-class			
	Subadult female	Subadult male	Adult female	Adult male
≤12.5	0.450	0.184	0.356	0.010
12.5–14.5	0.139	0.235	0.477	0.149
>14.5	0.000	0.156	0.084	0.760

accompanying dependent young. These differentiations are of potential value in ecological research. Large males often have strong influences on the behaviors and distributions of other bears, especially smaller subadult males and females with young (Mattson et al. 1987, 1992, Weilgus 1993). The large size of adult males also engenders constraints and opportunities unique to this class that affect their use of certain foods such as roots and ungulate tissue (Mattson 2000). Reproductive females are demographically the most important type of bear (Knight and Eberhardt 1985, Pease and Mattson 1999). Moreover, not only do they cope with especially onerous energetic demands (Mattson 1990), they also exhibit sometimes high levels of risk-sensitive foraging (Weilgus 1993, Mattson 2000) due to the potential for infanticide, especially by adult males (McLellan 1994).

Tracks also promise to be useful in studying behaviors highly associated with trackable substrates. In the Yellowstone region, these behaviors include excavating roots or rodents and rodent food caches and fishing for spawning trout. Foraging that involves excavation of soil logically leads not only to the creation of trackable substrate but also the juxtaposition of feet and loose, finer-textured soil. Reinhart and Mattson (1990) demonstrated the potential use of tracks in studying bear fishing behavior, which often leads bears to be active on highly trackable streamside substrates. The sparseness of tracks at sites where bears had excavated red squirrel (*Tamiasciurus hudsonicus*) middens for whitebark pine seeds or dirt and debris hills for ants was likely due to sparse trackable substrates associated with the prevalence of spongy organic debris at the former and organic debris combined with coarse-textured soil at the latter. The relative sparseness of tracks at excavated beds plausibly was due to their erasure by ground pressure and abrasion from the recumbent bear(s).

Application of these results to research or management situations entails several steps. Track measurements should be corrected for size-related bias by applying equations [1] or [2] to derive "pseudo-pad" measurements. Pseudo-pad sizes could then simply be related to the pad-size categories given in Table 2, and inferences made based on the associated probabilities of gender and age-class membership. Alternatively, pseudo-pad measurements could be introduced into all 4 of the class-specific equations in Table 1 to derive logit-transformed probabilities of membership in each class. Actual probabilities (p) can be calculated by back-transforming the result of these equations (y), as follows: $p = e^y / (1 + e^y)$ (Demaris 1992).

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