BROWSE REMOVAL, PLANT CONDITION, AND TWINNING RATES BEFORE AND AFTER SHORT-TERM CHANGES IN MOOSE DENSITY

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ABSTRACT: We monitored forage-based indices of intraspecific competition at changing moose (*Alces alces*) densities to gauge short-term, density-dependent environmental feedback and to ultimately improve management of moose for elevated sustained yield. In 4 areas of interior Alaska where moose density recently changed, we evaluated the magnitude of change among 4 browse indices: proportional offtake of current annual growth biomass (OFTK), proportion of current twigs that were browsed (PTB), mean twig diameter at point of browsing (DPB), and proportion of plants with broomed architecture. In 1 area where moose density increased 100% in 6 years following effective predation control, browse removal increased 138% for OFTK, 20% for PTB, and 16–42% for DPB of primary browse species, with a 44% increase in brooming. We also studied 3 areas where moose density declined 31–41% following elevated antlerless harvests of 2–4 years duration. In these areas (with intervals of 3–12 years between browse surveys) we found declines of 30–40% in OFTK, 26–68% in PTB, and 11–37% in DPB, but changes in plant architecture were inconsistent. The proportion of parturient cows with neonate twins did not change between browse surveys, presumably because of a substantial lag time influenced by life history of the dominant reproductive cohorts and little change in browse nutrient content and digestibility. Of the 4 browse indices studied, proportional OFTK most consistently reflected the direction and magnitude of short-term changes in moose density. Area-specific measures of habitat and animal conditions at high moose density provided an objective means for gauging the capacity of the respective ecosystems to support moose and maintain forage plants. We used these measures of winter forage and moose condition to justify implementing harvest strategies and to ultimately reduce high moose densities below levels of strong negative feedback.

Key words: Alaska, density-dependent, forage, intraspecific competition, moose, nutritional condition.

Moose (*Alces alces*) management becomes increasingly challenging for populations at the extremes of the nutritional gradient. At low densities managers may consider predator control to increase abundance (Gasaway et al. 1992). At high densities habitat enhancement may be an option to increase forage, or antlerless harvests could reduce abundance or population growth rates (Boertje et al. 2009, Young and Boertje 2011). Wildlife managers in Alaska are often required to estimate harvestable surplus and nutritional status of wild moose populations over large areas (≤15,000 km²) of remote forested and subalpine habitats. It is difficult to estimate the

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capability of habitats to support moose because of limited studies on the physiological requirements based on captive animals (reviewed in Schwartz and Renecker 1997) and the inherent variability in habitat and other environmental factors. Biologists must either quantify forage production (kg/ha) in the context of daily food requirements for an absolute estimate of carrying capacity (e.g., Wolff and Zasada 1979, Crete 1989, MacCracken et al. 1997) or use indices to assess the relative nutritional status of the moose population and/or condition of the range.

There are no standardized economical methods for assessing landscape carrying capacity in remote areas of Alaska, so biologists use nutritional status of the moose population or indices related to winter forage use (Boertje et al. 2007, Seaton et al. 2011). These indices presumably reflect the negative feedback in nutrition from increased intraspecific competition for food resources at increasing moose density and indicate if competition is reduced as density declines. Negative feedback reduces productivity and thus sustainable harvest among age and sex classes (McCullough 1984), poses a heightened risk of unsustainable forage removal, and can lead to dramatic population declines, often facilitated through winter-related mortality (Gasaway et al. 1983). The most established index of nutritional status of a moose population in interior Alaska is twinning rate, the proportion of parturient females with 2 neonatal calves (Franzmann and Schwartz 1985, Keech et al. 2000, Boertje et al. 2007). Dressed weights of harvested calves (e.g., Cederlund et al. 1991), age at first reproduction, short-yearling live mass, and browse removal rate (Boertje et al. 2007) have also been used to estimate or gauge nutritional status of moose populations. However, few studies have examined how well these indices respond following intended changes in abundance through management actions.

Measuring animal indices can be constrained by sample size at low density, limiting their usefulness in monitoring change in abundance. It can be difficult or infeasible to observe an adequate sample of random parturient females from aircraft for estimating twinning rate in areas of low moose density (e.g., Stout 2010) or in dense cover that hinders viewing of calves. Conversely, browse sampling is not constrained by moose observations. Seaton et al. (2011) documented an inverse correlation between proportional browse biomass removal and twinning rate across a 10-fold range in density (0.1–1.2 moose/km^2) among 8 game management units of interior Alaska. That study demonstrated the utility of a habitat metric for indirectly judging nutritional condition of adult female moose, which helped substantiate prior conclusions by Boertje et al. (2007) based on smaller sample sizes. In this study we sought to document short-term, landscape-level changes in browse removal rates and architecture of winter forage species following short-term, management-induced changes in moose density.

Seaton (2002) reviewed methods of estimating browse removal by moose and used a modified technique to characterize "apparent" browse production (PROD; kg/ha above snow) and browse offtake by moose (OFTK; kg/ha), and to estimate proportional OFTK (OFTK/PROD). The technique quantifies woody biomass through measuring twig diameter at the proximal end of current annual growth (CAG) and the diameter at point of browsing (DPB) in late winter, just prior to the new growing season. Earlier studies reported a correspondence between proportional OFTK and the proportion of twigs browsed by moose (PTB = number of DPB > 0 divided by number of CAG) (Regelin et al. 1987, MacCracken and Viereck 1990), which suggested that the simpler twig count would be more efficient. However, Seaton (2002:32) cited another

study (K. Kielland and T. Osborne, unpublished data) where PTB was insensitive to a large (8-fold) change in moose abundance in western interior Alaska. Thus, estimating the biomass produced and removed with diameter measurements is important because moose may clip twigs at a range of diameters, and the nutritional value (e.g., digestibility and nutrient concentrations) decreases as CAG diameter increases (Vivås and Sæther 1987, Kielland and Osborne 1998). The smallest diameter twigs provide the most nutrient gain per unit of mass but extend rumen fill time, whereas the largest diameter twigs provide less nutrient gain per unit mass and extend rumen processing time (Gasaway and Coady 1974, Shipley and Spalinger 1992). Seaton (2002) also sought to incorporate forage plant architecture to gauge the longer-term effects of moose browsing. This information might additionally help managers and the public understand negative feedback at higher moose densities and characterize relatively less use at lower densities.

In this study we followed a recommendation by Seaton et al. (2011) to evaluate the utility of browse indices for detecting short-term changes in intraspecific competition following intended management actions. In 4 areas with baseline browse data and subsequent changes in moose density, we examined the magnitude of changes in browse removal and plant architecture as gauges of density-dependent feedback. We compared changes in browse metrics with changes in an established index of nutrition (twinning rates) to better understand how browse removal may or may not reflect changes in moose nutrition. We assumed that reducing moose abundance in a defined area where forage production changed relatively little over time will reduce intraspecific competition for preferred species, with an inverse response following an increase in abundance. We predicted that increased moose density would cause increased proportional OFTK, increased PTB, increased mean DPB for at least the dominant or preferred browse species, and an increased proportion of plants with architecture partly or heavily affected by moose foraging. These conditions are presumed to be coincident with a decrease in moose nutrition, resulting in a lower twinning rate at higher density. Where moose density decreased, we predicted the inverse responses, with one exception; that short-term reversal of trend in plant architecture as affected by moose browsing at high density (broomed → unbrowsed) would be unlikely on existing plants in the absence of widespread disturbance to regenerate young plants, such as fire or flooding. Also, moose nutrition, as indexed by twinning rates, would not likely increase immediately following a decline in moose abundance unless browse quantity and quality increased substantially. Intentionally changing reproductive rates is more likely a long-term proposition based on changing calf weights and eventually the life history of the dominant reproductive cohorts (females 4–10 yr old; Boertje et al. 2007).

STUDY AREAS AND MOOSE ABUNDANCE

The 4 study areas (Unit 19D, Unit 20A Central Hills, Unit 20A Western Flats, and Unit 20D) were located in the boreal forest of interior Alaska, USA (Seaton et al. 2011, Fig. 1). Management actions were implemented in these areas to influence moose abundance. To illustrate the magnitude of density change in each area, we calculated moose abundance and confidence intervals for areas approximating the extent of browse sampling before and after management actions.

Population Increase

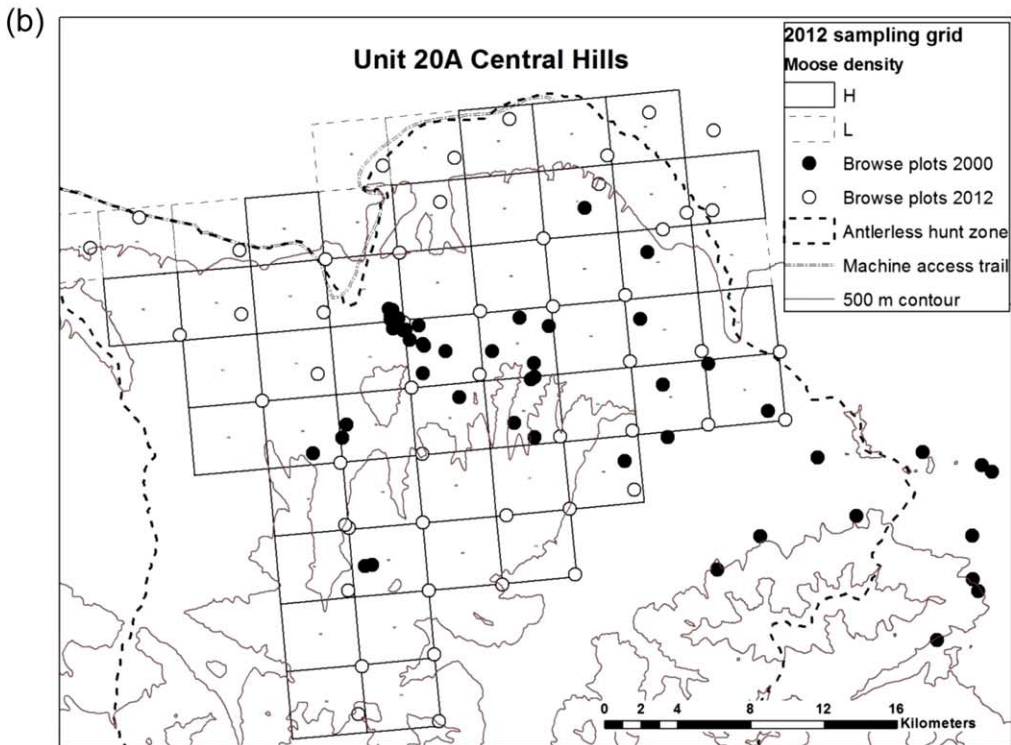Unit 19D in the remote Kuskokwim Valley is comprised of large floodplains and
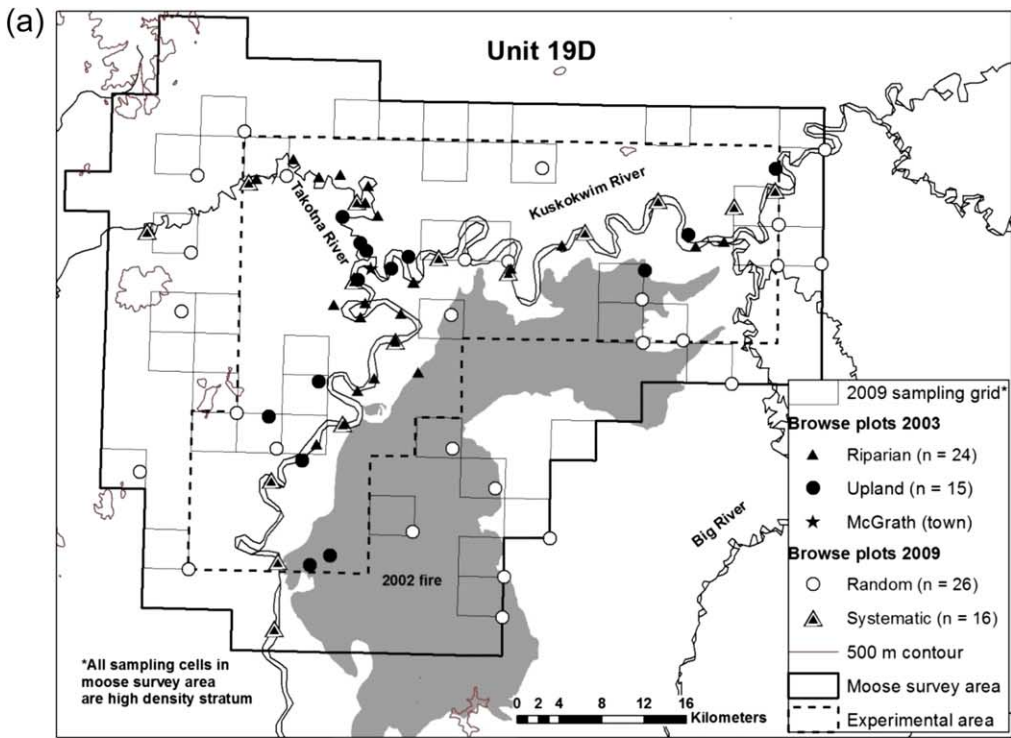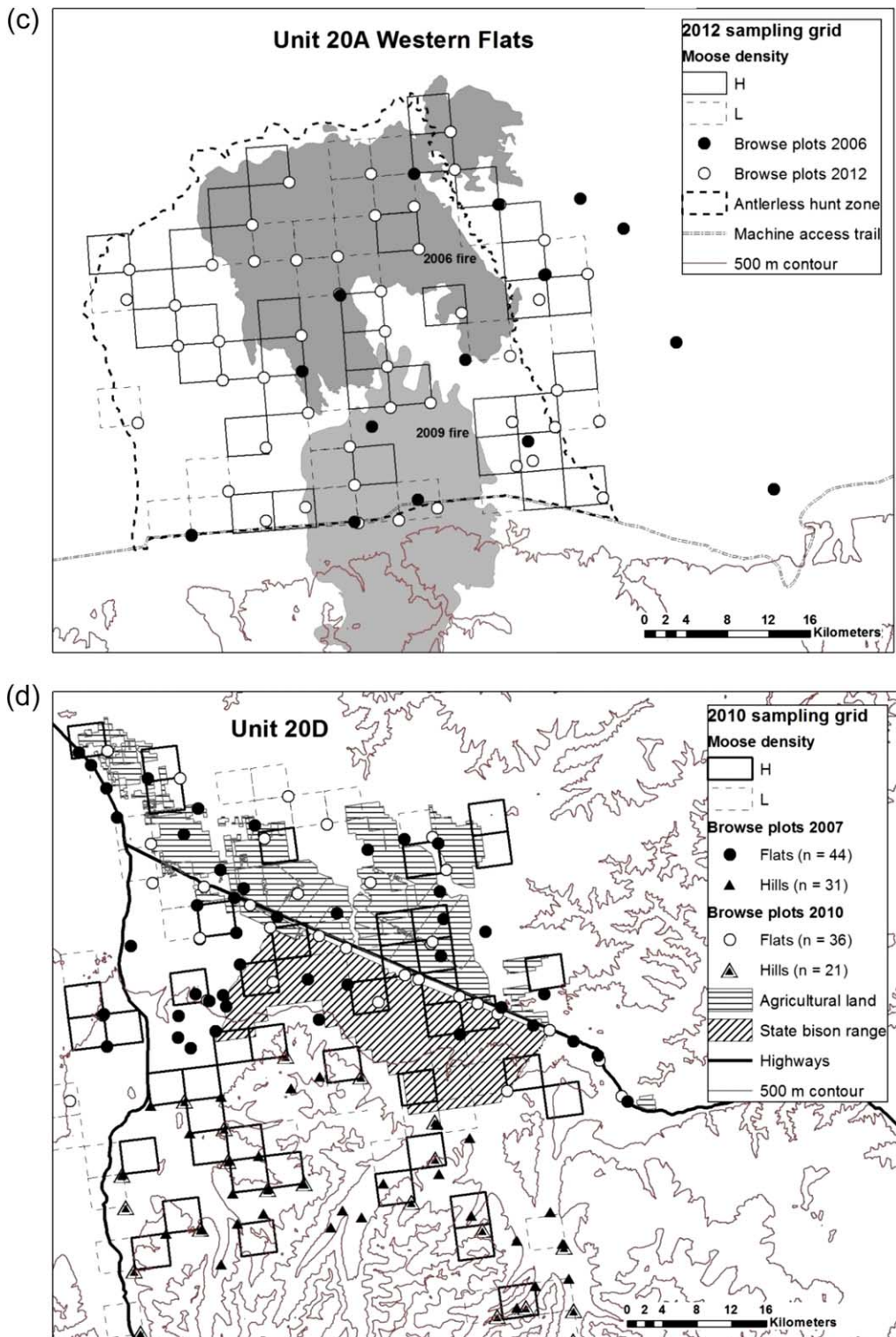
Fig. 1. Continued on next page.

Fig. 1. Post-treatment sampling grids and browse plot locations before and after management actions intended to affect moose density for the 4 study areas in Interior Alaska.

forested uplands within 40 km of McGrath (62° 57′ N, 155° 36′ W). In this study area we sampled browse on 3 occasions: broadly over 10,600 km² in 2001, narrowly in a 1368 km² experimental area (Keech et al. 2011) in 2003, and over a 2896 km² moose survey area that included the experimental area in 2009 (Keech 2012). We used the 2003 browse data for pre-treatment in Unit 19D because sampling scale (Paragi et al. 2008:36) was closer to that from 2009 (Fig. 1a), but we provided 2001 data for additional pre-treatment context on variation in browse metrics when moose density was low (Paragi et al. 2008:9). In Unit 19D, Keech et al. (2011) described predation control beginning in 2003 that caused a gradual increase in moose abundance over the next 6 years. In the 2009 browse sampling area, moose density estimated from fall aerial surveys doubled from 0.30/km² in 2001 to 0.62/km² by 2009 (Keech 2012:14).

Population Decrease

Units 20A and 20D are near the road system in the Tanana Valley near the city of Fairbanks and the town of Delta Junction, respectively. The Unit 20A Central Hills study area was comprised of forested uplands and subalpine shrubs 100 km south of Fairbanks in the foothills of the Alaska Range (64° 08′ N, 147° 55′ W). This area was primarily used during fall and winter by moose that migrated to lowland flats to the north during the summer (Keech et al. 2000), inclusive of when hunting and abundance surveys occurred. We sampled 600 km² of the Unit 20A Central Hills as part of a larger study by Seaton (2002) in 2000 and sampled 790 km² in 2012 that conformed to a harvest-reporting boundary and largely overlapped the earlier browse-sampling area (Fig. 1b).

The Unit 20A Western Flats (64° 26′ N, 148° 50′ W) were forested lowlands with interspersed wetlands. We sampled 1100 km² of the Western Flats in 2006 and 1625 km² in 2009; the latter survey largely overlapped the earlier survey area, but nearly half of it was influenced by large fires in 2006 and 2009 (Fig. 1c). The Unit 20D study area (63° 46′ N, 145° 15′ W) varied from agricultural lands and forest with several upland areas that had burned in the last 20 years near Delta Junction to subalpine scrub in the foothills of the Alaska Range 50 km south. We sampled browse in southwestern Unit 20D over 3250 km² in 2007 and 2010 (Fig. 1d).

In Unit 20A, antlerless harvests were implemented or expanded to reduce moose abundance during 2004–07 by use of hunt zones and extended seasons, including the Central Hills and Western Flats (Young and Boertje 2011). We subsampled data from the larger Unit 20A surveys before and after antlerless harvests to estimate *post hoc* moose abundance in browse survey areas in the hills and flats (Kellie and DeLong 2006). In southwest Unit 20D, antlerless harvest reduced moose abundance in fall 2007 (DuBois 2008:397) and fall 2008 (DuBois 2010:390). The Unit 20D antlerless hunts were short duration prior to substantive snowfall, with female harvest predominantly occurring in the lowland flats north of the foothills (S. DuBois, unpublished data) that were accessible by all-terrain vehicles. Similar to the abundance estimates for Unit 19D (Keech et al. 2011, Keech 2012), in the other 3 study areas we multiplied estimated abundance by a sightability correction factor (SCF) for moose not observed using radio-marked individuals. We used SCF = 1.21 for Unit 20A (Boertje et al. 2009) and SCF = 1.1 for Unit 20D (S. DuBois, unpublished data), and the SCF variance was incorporated with that of the GeoSpatial Population Estimator (GSPE; Kellie and DeLong 2006) into 90% confidence limits (Goodman 1960, Keech et al. 2011).

METHODS

Browse Removal

We used moose distribution from fall abundance surveys during shallow (<40 cm) snow as the sampling extent for browse surveys and attempted to minimize sampling bias at the landscape and vegetative stand scales. Our landscape sampling design and procedures for selecting plot locations began with pre-selected random points among vegetation strata (Seaton 2002) but evolved with logistical experience in the field (Paragi et al. 2008:2–4). Since 2006 we have primarily used rectangular GSPE cells based on 2 minutes of latitude and 5 minutes of longitude (ca. 3.7 × 4.1 km) from recent moose surveys for stratified random sampling at a 3:2 ratio of high:low moose density (e.g., Kellie and DeLong 2006:21). Most plot access in remote areas was by helicopter, but we used vehicles where portions of Unit 20D were near a highway or forest road (Paragi et al. 2008:4).

The landscape sampling protocol was developed in boreal forest, but we accommodated the linear nature of riparian browse distribution when we began sampling subalpine habitats. The helicopter flew on the designated course within GSPE cells until the first patch of browse ≥0.5 m tall and above snow was encountered, at which point we selected a randomized distance (30–100 m from the nearest safe landing spot) and direction (3 tries to select a site with browse before sampling cell was skipped) for choosing the plot center in the vegetation stand. One exception to stratified sampling with GSPE cells was the addition in 2009 of *ad hoc* systematic plots to ensure adequate sampling of the riparian zone along the Kuskokwim River and Takotna River in Unit 19D for comparison to earlier sampling stratified by vegetation type (Paragi et al. 2008). We chose a random starting point along the Kuskokwim River near the eastern boundary of the sampling area and landed at the nearest willow bar every 10 km downriver (straight line by helicopter) and also every 10 km upriver on the Takotna from its confluence. In 2012 we began defining study areas in Unit 20A by polygon boundaries based on drainages that are used for cataloging moose harvest location from hunter reports so that inference about browse could be more directly related to changes in reported harvest.

Our objective was to sample at least 30 plots per study area with browse above snow to optimize precision and cost (Seaton et al. 2011), so we typically selected at least 40 sample cells because some random plot locations near helicopter landing spots do not contain browse. This sample size was not achieved in Unit 20A Western Flats in 2006, where we omitted several sites due to absence of browse near safe landing zones. However, the 15 plots achieved in this survey (Table 1) are expected to accurately reflect the biomass removal level but with potentially high variance (Seaton et al. 2011, Fig. 3). Where clumps of randomly chosen sample cells occur, sampling at least one cell in the clump provided landscape coverage if logistics became limiting (e.g., degraded flying weather or distance from fuel).

We analyzed proportional OFTK over the winter to describe the interaction between moose and their winter forage. The rationale for plot sampling and browse metric analysis is described elsewhere (Seaton 2002, Paragi et al. 2008). Snow depth >70 cm can restrict access to forage, increase energetic requirements for locomotion, and influence habitat selection; snow depth >90 cm greatly restricts movement, potentially hindering adequate forage intake (Coady 1974). Consequently, we recorded snow depth at plots during browse surveys for a context of winter severity, particularly as a confounding factor between sampling events. We sampled only plants above snow

Table 1. Sampling details and estimates of apparent browse production (sampled twigs above snow extrapolated to plot composition) by study area within game management units in interior Alaska.

Game Management Unit	Browse sampling year	Sampling area (km²)	Browse samples (n)			Apparent production (kg / ha)	
			Plots	Plants	Twigs	$\bar{x}$	95% CI
19D	2001	10,600	36	251	2420	201	19
19D	2003	1368	39	298	2377	689	52
19D	2009	2896	42	278	2746	343	26
20A C. Hills	2000	600	49	235	2504	745	154
20A C. Hills	2012	790	37	177	1799	30	3.8
20A W. Flats	2006	1100	15	109	1099	75	9.0
20A W. Flats	2012	1625	44	312	2945	14	1.0
20D	2007	3250	75	437	4312	52	4.7
20D	2010	3250	57	431	4108	73	8.0

with measurable CAG between 0.5 and 3.0 m above ground level in a 15-m radius plot near the end of browse removal in late winter (late March or early April, before leaf emergence). We randomly selected 3 plants per species present, using plants as the sample unit for inference on browse removal at the scale of study area. Plant taxonomy followed Collet (2004) for willows and Viereck and Little (2007) for other species, with winter willow identification aided by an unpublished guide (D. Simpson, Alaska Department of Fish and Game [ADFG] 1986).

For each randomly selected plant within a species, we randomly selected 10 twigs. For each twig we recorded to 0.1 mm precision the DPB if applicable, and CAG (Lyon 1970). We then counted the total number of twigs with CAG on each of the 3 plants. We used the regression coefficients relating diameter to dry mass (Paragi et al. 2008:40–41) and the number of twigs with CAG per plant to estimate PROD and OFTK (Telfer 1969). An exception was *Salix lasiandra* for which 3 plants were measured on each of 2 plots in Unit 20A Western Flats in 2006. We did not have a regression

equation for *S. lasiandra*, so we used *S. bebbiana* equations for biomass analysis because these twigs have a similar morphology. We estimated OFTK based on sampled twigs only (mean twig per sampled plant) with plants as the sample unit. We extrapolated PROD and OFTK from sampled twigs to the plot level for comparison among study areas, recognizing that this may introduce sampling bias through variation in the proportion of total plants sampled per species and variability in plant counts within plots.

We used software written in R language (R Development Core Team 2008, Version 2.1.1; code and instructions available under project 5.10 at <http://www.adfg.alaska.gov/index.cfm?adfg=librarypublications.wildlife research#habitat> to read a Microsoft® Access® (version 2003) database containing plot counts, twig diameters, diameter–biomass pairs, and dry-weight conversions. We used this software to estimate the diameter–biomass relationships, PROD, and OFTK on the basis of plant, species, plot, and study area (Paragi et al. 2008). We applied binomial 95% confidence limits (Cochran 1977:58) with *n* as the number of plants measured, rather than twigs, to avoid

pseudo-replication (unequal proportion of plants sampled per species and per plot) and to portray a more conservative variation. Where moose density changed between browse evaluation periods, we evaluated significant probability of increase or decrease in twig metrics with 1-tailed tests, where direction of change associated with removal was predicted to be the same as direction of change in moose abundance. We tested for difference between proportions of OFTK and of PTB using a z-test (Zar 1984:396) with the smaller number of plants for degrees of freedom in the t distribution. We tested for difference in snow depth and in DPB before and after management actions for each browse species using Mann-Whitney U (Conover 1980) because data distributions were often non-normal (Lilliefor's test, $P < 0.05$).

Browse Architecture

Seaton (2002:19) classified forage plants based on their history of browsing by moose and the resulting compensatory growth, termed "architecture." In contrast to removal of CAG in a specific winter, architecture describes multi-year growth history and is unidirectional (unbrowsed → browsed → broomed) unless disturbance resets plants to an unbrowsed canopy. Thus, in addition to historic moose density, architecture in study areas is influenced by fire or vegetation management in prior years that stimulates young growth. Three categories of plant architecture were defined from evidence of browsing prior to the current year for each plant: "unbrowsed" (no evidence of browsing prior to the current year); "browsed" (browsing in past years but <50% CAG twigs between 0.5 and 3.0 m arose from lateral stems that were produced as a result of browsing); and "broomed" (>50% of CAG twigs between 0.5 and 3.0 m arose as lateral stems). To reduce measurement error, architecture was classified by the first 3 authors or under their

direct supervision. We used a Chi-square test for independence in proportions of the plant architecture classes and portrayed variation in the proportions of plants in architecture classes with binomial confidence limits using n as the number of plants.

Twinning Rate

Boertje et al. (2007) described estimation of moose twinning rates from aerial surveys shortly after peak of calving in late May. We obtained data from area or research biologists that conducted surveys annually in our 4 study areas. To evaluate trend in twinning rate, we used R script to estimate the mean rate and 95% confidence limits using a parametric bootstrap (100,000 repetitions).

RESULTS

Moose density in the Unit 20A Central Hills was 2.4 moose/km^2 prior to antlerless harvest and was reduced 33% by the 2nd browse survey (Table 2). The 2003 abundance estimate likely represented the peak density 3 years after the first browse survey in 2000 as inferred from abundance estimates in the larger Unit 20A (Young and Boertje 2011); thus, moose density during the first browse survey may have been slightly lower. The 2012 abundance estimate was 5 years after the end of liberal antlerless harvest, a period of reduced and comparatively stable moose abundance in all of Unit 20A (Young 2012, Table 2).

In Unit 20A Western Flats, the evidence for a 31% decline in density from 1.2 moose/km^2 in 2006 was weaker because the estimate had twice the proportional variance of the other study areas (Table 2). The 2006 browse survey occurred after 2 years of liberal antlerless harvest, thus likely reflected a reduced moose density (lesser expected difference in browse removal) from the peak in fall 2003 for all of Unit 20A (Young and Boertje 2011). This population may have experienced a relatively smaller change in

Table 2. Estimates of moose density and browse removal (sampled twigs only) by moose reported by study area within game management units in interior Alaska. Moose abundance surveys were in early winter prior to the associated browse surveys unless otherwise noted. Proportions of offtake and twigs browsed were predicted to change in the direction of trend in moose density.

Game Management Unit	Browse survey year	Moose density (no./km^2)		Proportional browse offtake		Proportion of twigs browsed	
		$\bar{x}$	90% CL	$\bar{x}$	95% CL[a]	Prop.	95% CI
19D	2001	0.30	0.25, 0.35	0.159	0.112, 0.195	0.110	0.039
19D	2003	0.30[b]	0.25, 0.35	0.171	0.144, 0.221	0.287	0.051
19D	2009	0.62	0.48, 0.72	0.405	0.332, 0.471	0.346	0.056
20A Central Hills	2000	2.36[c]	1.84, 2.87	0.433	0.394, 0.462	0.401	0.063
20A Central Hills	2012	1.59	1.32, 1.86	0.303	0.227, 0.357	0.130	0.050
20A Western Flats	2006	1.19	0.71, 1.68	0.307	0.112, 0.442	0.161	0.069
20A Western Flats	2012	0.82	0.50, 1.14	0.190	0.147, 0.228	0.119	0.036
20D	2007	2.11	1.63, 2.60	0.253	0.191, 0.323	0.167	0.035
20D	2010	1.24	1.00, 1.48	0.153	0.106, 0.199	0.117	0.030

[a]Bootstrapped confidence intervals may be asymmetrical.
[b]Density in fall 2003 assumed to be similar to that from survey in fall 2001 (Keech 2012:13–14).
[c]Survey in fall 2003; this was likely the period of maximum abundance prior to liberal antlerless harvest (Young and Boertje 2011, Fig. 2) and the closest period with enough abundance sample units in the browse study area to permit a *post hoc* analysis. For comparison, the estimate with visibility correction for all of Unit 20A (12,900 km^2 of moose habitat <1350 m elevation) was 1.05 moose/km^2 in 1999 (prior to 1st browse survey); 1.37 moose/km^2 in 2003 (prior to liberal antlerless harvest); 0.98 moose/km^2 in 2008 (after liberal antlerless harvest), and 0.98 moose/km^2 in 2011 (prior to 2nd browse survey) (Young 2012, Table 2).

abundance than the other 3 study areas, so we expected that the magnitude of change in browse metrics and twinning rate might be ambiguous with respect to the other 3 study areas. Moose density in Unit 20D was 2.1 moose/km^2 before antlerless harvest; and was reduced 41% by 2010.

Willows (*Salix* spp.) dominated or co-dominated apparent browse production in most instances (Fig. 2). *S. alaxensis* composed the majority of browse biomass in active riparian floodplains regardless of elevation (e.g., including incised drainages in subalpine), whereas *S. pulchra* often dominated or co-dominated production with *Betula neoalaskana* or *Populus tremuloides* in upland sites, particularly after recent fires or logging. PROD ranged greatly among study areas and within study areas between years (14–745 kg/ha; Table 1). Within a

study area, the greatest change was in Unit 20A Central Hills that was possibly influenced by different browse sampling stratifications before and after antlerless harvest. Sampling in the 2000 browse survey in the 20A Central Hills included 1 plot of extremely high production (22,148 kg/ha; Paragi et al. 2008:53) that boosted mean apparent production from 329 to 745 kg/ha. Lower PROD in post-treatment browse surveys for Units 19D and 20A Western Flats may also reflect slow vegetative recovery from recent fires (Fig. 2a and 2c). OFTK exceeded 45% for dominant willow species at higher moose densities within study areas (Fig. 2): *S. alaxensis* in Unit 19D (2009) and Unit 20A Central Hills (2000), and *S. pulchra* in Unit 20A Central Hills (2000) and Unit 20A western flats (2006). Mean snow depth (7–33 cm) during browse surveys differed little between
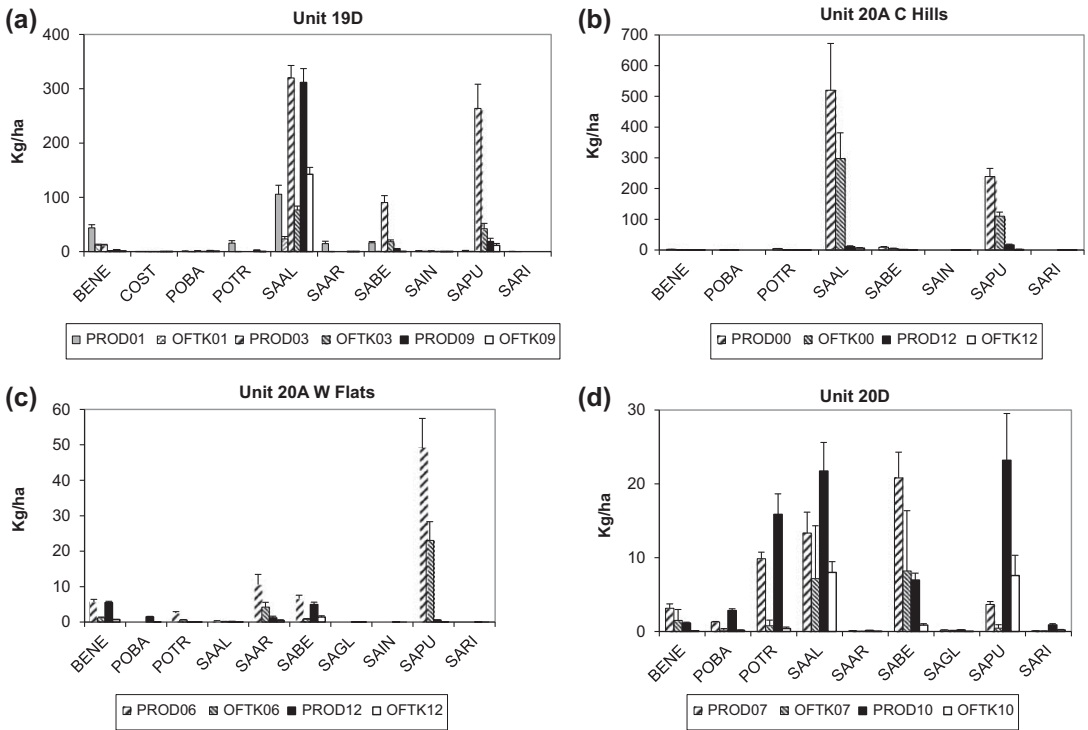
Fig. 2. Apparent production (PROD) and offtake (OFTK; both in kg/ha) as extrapolated from sampled twigs to plot composition in 4 study areas within interior Alaska. Moose abundance increased (Unit 19D) or decreased (all others) coincident with intended outcome of management actions. Years of PROD and OFTK are represented by last 2 digits of year starting with 2000. Note differences in *y*-axis scale among areas; error bars are 95% confidence limits. An additional year of pre-treatment data (2001) was available for comparison in Unit 19D. Species codes: BENE (*Betula neoalaskana;* formerly *B. papyrifera*), COST (*Cornus stolonifera*), POBA (*Populus balsamifera*), POTR (*P. tremuloides*), SAAL (*Salix alaxensis),* SAAR *(S. arbusculoides),* SABE *(S. bebbiana)*, SAGL (*S. glauca*), SAIN (*S. interior*), SAPU (*S. pulchra*), and SARI (*S. richardsonii*).

sampling periods within study areas and remained <70 cm by late winter in 3 of 4 study areas. Unit 19D was the exception where mean snow depth for the winter post-treatment (107 cm) was 56 cm higher than pre-treatment (Mann-Whitney $U = 18$, $P < 0.001$).

OFTK was more consistent and precise than PTB in reflecting direction and magnitude of changes in moose density, or lack thereof. Change in OFTK from before to after management actions (Table 2) was significant in all 4 areas and in the expected direction of change in moose density ($z \geq$

2.7, $P < 0.01$, 1-tailed). Change in PTB (Table 2) was significant for Unit 20A Central Hills ($z = 6.0$, $P < 0.0005$) and Unit 20D ($z = 2.1$, $0.01 < P < 0.025$), but not for Unit 19D ($z = 1.5$, $0.05 < P < 0.1$) or Unit 20A Western Flats ($z = 1.1$, $0.2 < P < 0.5$). Whereas the pre-treatment moose density was similar between the 2001 and 2003 browse surveys in Unit 19D (0.38 and 0.41 moose/km² in the smaller 2003 browse study area; Keech 2012:13), the lack of difference in OFTK ($z = 0.35$, $P > 0.5$) was in marked contrast with the unexpected difference in PTB ($z = 6.2$, $P < 0.001$, 2-tailed; Table 2).

Further, PTB was highly variable for various degrees of OFTK whether a moose population increased or decreased (Fig. 3).

Direction of species-level change in DPB generally corresponded with the direction of change in both OFTK and PTB. The strongest correspondence existed for those species composing the dominant (or co-dominant) biomass in a study area (Table 3). Among the 4 study areas, proportional
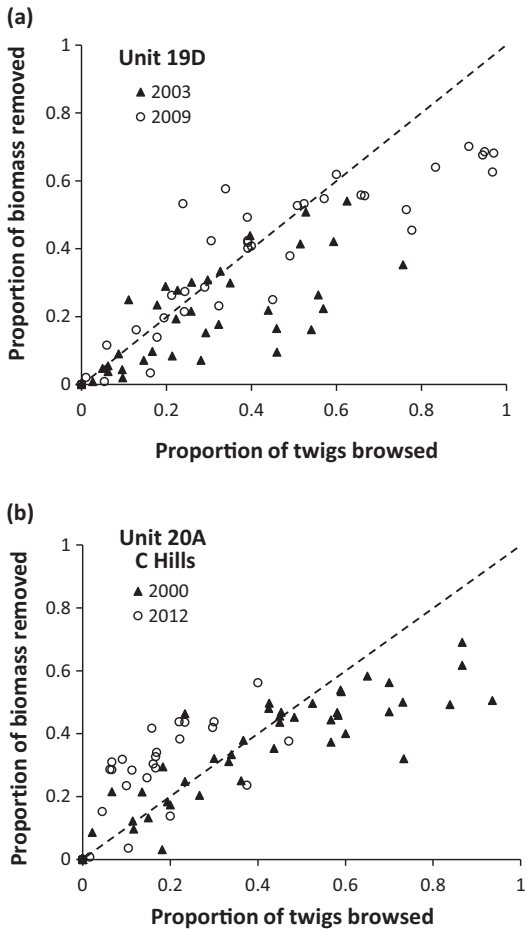
(a)

(b)

Fig. 3. Examples of greater range in proportion of twigs browsed for a given range of offtake where moose populations had increased (a) and decreased (b) in interior Alaska. The dashed lines illustrate a 1:1 relationship for comparison to the year-specific plot data.

magnitude of change in DPB ($P < 0.05$ by species) was 11–35% ($\bar{x} = 22\%$, n = 6) in the predicted direction for each study area. The relative importance of DPB as a component of OFTK is evident in scaling among browse metrics during the 100% increase in moose in Unit 19D; 138% increase in OFTK corresponded to increases of 20% in PTB (all species combined) and 16–42% in DPB of the primary browse species. Where moose density decreased 31–41% in the other 3 study areas, decreases were documented in OFTK (30% in Unit 20A Central Hills to 40% in Unit 20D), PTB (26% in Unit 20A Western Flats to 68% in Unit 20A Central Hills), and DPB of the primary browse species (11–37%, both extremes in Unit 20D).

Plant architecture also responded to changes in moose density. There was a 44% increase in broomed plants following a moose population increase in Unit 19D (Fig. 4). In the absence of vegetative disturbance such as fire, the proportion of unbrowsed plants increased 6-fold (2% to 16%) in the Unit 20A Central Hills after the moose population declined from the highest density in our 4 study areas; this was also the longest period between end of liberal antlerless harvest (presumed greatest point of density reduction; Table 2) and the post-treatment browse survey (5 years later). There was an 83% increase in proportion of unbrowsed plants in Unit 20A Western Flats following a reduction in moose density, where fires created new unbrowsed plants during and after antlerless hunts. However, we found no change in plant architecture in Unit 20D (Fig. 4) despite a 41% decline in moose density over 3 years. When compared with the 4 browse metrics, twinning rate showed no changes or trend in these moose populations during the intervening period of reduced moose density between browse surveys or soon thereafter (Fig. 5).

Table 3. Change in mean diameter (mm) at point of browsing (DPB) by moose on the primary winter forage species in areas where moose populations increased (Unit 19D, 2003–09) or decreased (all others) in accordance with intended outcome of management actions, interior Alaska. DPB was predicted to change in the direction of trend in moose abundance. Bold text represents dominant species (>50% of total estimated apparent production extrapolated from sampled plants to plot). Trend in DPB (positive or negative) is inferred from the Mann-Whitney U statistic ($P < 0.05$). An additional year of pre-treatment data (2001) in Unit 19D is shown for comparison. Species codes: BENE (*Betula neoalaskana*), SAAL (*Salix alaxensis*), SABE (*S. bebbiana*), and SAPU (*S. pulchra*).

Area	Year	BENE	SAAL	SABE	SAPU
Unit 19D	2001	2.7	**3.9**	3.0	2.1
Unit 19D	2003	2.8	**4.3**	3.4	**3.2**
Unit 19D	2009	3.0	**5.0**	3.2	3.1
Trend		none	pos	none	none
P		0.43	<0.001	0.11	0.7
Unit 20A Central Hills	2000	2.9	**4.3**	3.3	3.2
Unit 20A Central Hills	2012	2.8	**4.7**	3.2	**2.5**
Trend		none	none	none	neg
P		0.67	0.28	0.2	<0.001
Unit 20A Western Flats	2006	3.1	5.2	2.8	**3.2**
Unit 20A Western Flats	2012	**2.8**	3.4	**2.6**	2.2
Trend		none	neg	none	neg
P		0.06	0.03	0.25	<0.001
Unit 20D	2007	2.5	**4.5**	**2.4**	2.8
Unit 20D	2010	2.5	**3.8**	2.6	**2.5**
Trend		none	neg	none	neg
P		0.58	<0.001	0.32	<0.001

DISCUSSION

Proportional OFTK was a more comprehensive metric than PTB or DPB for detecting short-term, landscape-level changes in intraspecific competition for winter forage and potential effects on plants following management actions intended to affect moose density. Proportional OFTK consistently reflected change in moose density despite substantial variation in PROD (total and among species) before and after management actions. We infer this relationship of OFTK and density change as evidence that *proportional* OFTK is unbiased, likely because moose distribution reflects browse distribution and OFTK reflects available PROD. Our estimates of PROD and OFTK were complicated by 4 factors: 1) a change in landscape sampling design between pre- and post-treatment for Unit 19D and Unit 20A Central Hills, 2) by differences in size of some pre- and post-treatment study areas because of changing management issues, 3) by measuring a relatively limited number of plots over large diverse landscapes that met precision objectives for proportional OFTK (Seaton et al. 2011) but increased chance of sampling error, and 4) by measuring a limited number of forage plants without regard to nutrition or digestibility.

We attribute the relatively high variation in the relationship between OFTK and PTB (Fig. 3) to condensing species with different twig diameters to a simple count of browsed

twigs of all species combined. The effect of seemingly small change in DPB is relatively more important than changes in PTB in

explaining change in OFTK because the species-specific mass-diameter relationship is based on non-linear twig geometry that
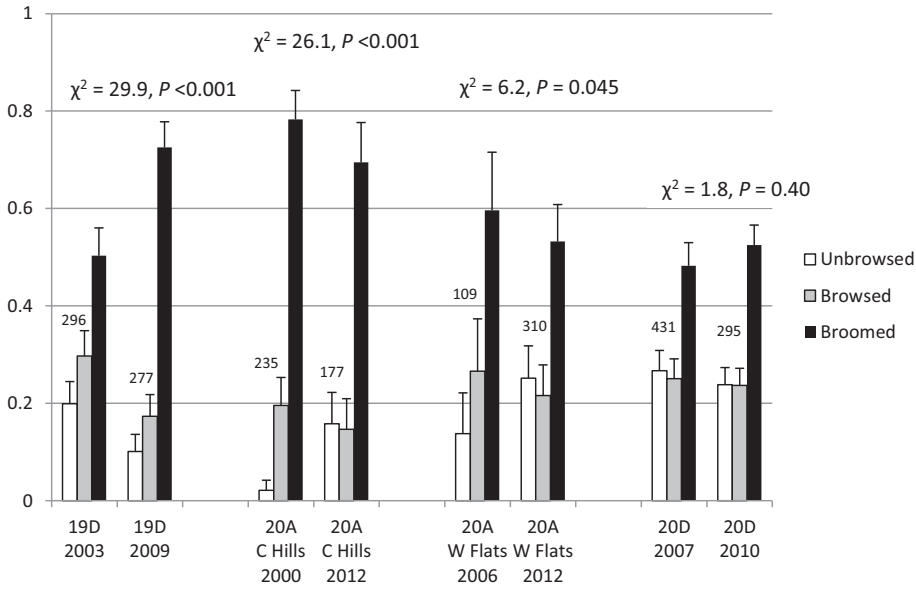

Fig. 4. The proportional changes in categories of browse plant architecture where the moose populations increased (Unit 19D) or decreased (all others) coincident with the intended outcome of management actions in interior Alaska. The binomial confidence interval (95%) and sample size are shown above bars.
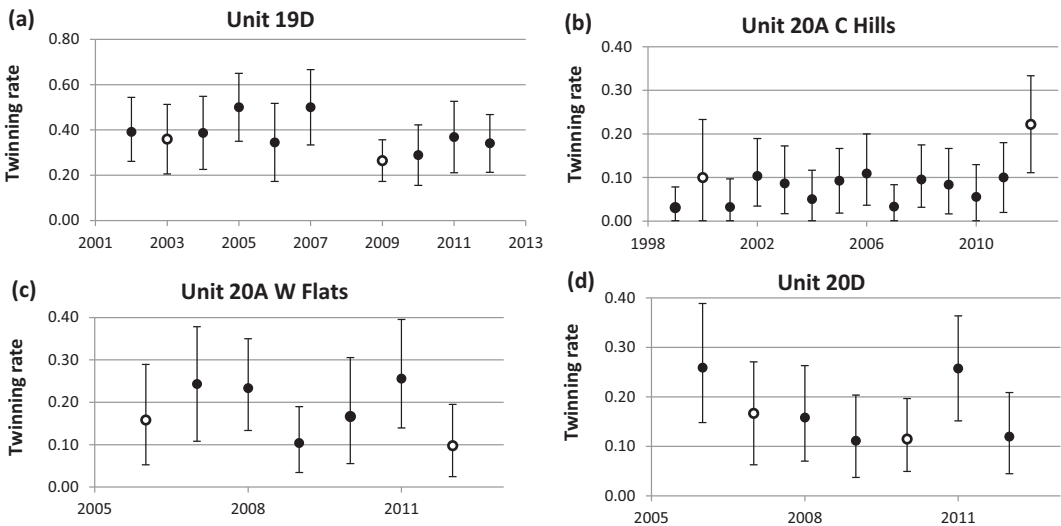

Fig. 5. Moose twinning rates in late spring for (a) 1 moose population that increased and (b-d) 3 populations that decreased coincident with intended outcome of management actions in interior Alaska. Open circles indicate years of browse surveys; confidence intervals were 95% bootstrapped.

does not scale equally with the linear proportion of twigs browsed. Our data may be the first to report how changes in moose foraging behavior, as shown by changes in stem cropping diameter (DPB), is influenced by moose density across a broad geographic range. These observational and experimental data strongly suggest that variation in DPB reflects variation in competition which translates into variation in demographic processes (e.g., twinning rates). However, DPB of several species is not readily condensed to a single numeric score, and using DPB in isolation could complicate comparisons of browse removal before and after management actions if preferences for forage species change over time. OFTK incorporates both PTB and DPB, thus reduces potential confounding of either component alone.

Over relatively short periods of change in moose density (2 years in Unit 20D to 6 years in Unit 19D), we expected change in architecture reflecting plant life histories to lag behind (or be of lesser magnitude) than change in the 3 metrics based on CAG and DPB. However, magnitude of changes in architecture reflecting increases in moose density (more broomed plants) or decreases in moose density (more unbrowsed plants) were often of equal magnitude to change in CAG and DPB metrics in as few as 5 years after change in density (Unit 20A Western Flats). This rate of change is comparable to recovery of broomed willows after elk (*Cervus elaphus*) reductions in Wyoming (Singer and Zeigenfuss 2003:80–81). The lack of architectural changes in Unit 20D despite a 41% decline in moose density may be explained by mismatch in scale of abundance surveys and distribution of antlerless harvest, where the latter primarily occurred in the flat and relatively accessible northern portion of the study area (S. DuBois, unpubl. data). We had stratified Unit 20D for browse surveys into flats and hills (sampling design

before liberal antlerless harvest described in Paragi et al. [2008]) and found no change in browse plant architecture in the flats. However, we noted a significant increase in brooming in the hills (T. Paragi, unpublished data), indicating the continued effect of high browsing pressure where moose density had not been reduced. This experience highlighted the importance of scaling the browse sampling appropriately to the extent of abundance estimates and management actions.

Browse removal rate at the moose population level is not an absolute measure of carrying capacity for a given moose density, nor a meaningful demographic parameter linked in real time to changes in birth and death rates. Browse removal rate is best used in concert with nutritional indices such as twinning rate that are also demographic parameters conveying population status relative to carrying capacity. Singer and Zeigenfuss (2003:67–70) studied consumption of willows as a product of percent leader use and percent twig use and found that moose density alone had little value in describing willow consumption where moose ($\bar{x}$ = 1.9/km^2) shared winter range with elk ($\bar{x}$ = 16.3/km^2) in Wyoming. Similarly, Månsson (2009) found no positive relationship between *Betula* spp. biomass removal and moose density where biomass removal of the dominant browse species, Scots pine (*Pinus sylvestris*), was related to moose density in Sweden. However, we found that OFTK of all browse species combined correlated with the direction and magnitude of moose density change. The highest biomass removal for all species combined approached 45% of CAG where moose density was highest (Unit 20A Central Hills).

We have focused on how browse removal relates to animal condition, but high levels of offtake warrant consideration of sustainable plant health or productivity as another trigger for habitat enhancement or prudent reduction in herbivore density.

Low to moderate levels of browse removal can stimulate browse production (Suter 1992), but removal beyond a threshold causes decline in production (Danell et al. 1985, Persson et al. 2005a). Persson et al. (2007) found that production response of *Betula* spp. to simulated browsing in northern Sweden was highest at 25–40% biomass removal (representing ca. 3 moose/km^2 on the winter range) on sites with moderate to high soil nutrients but lower on sites with low soil nutrients. Singer and Zeigenfuss (2003:70) observed a range (0–47%) in willow removal among study sites, with the highest growth response occurring at moderate (ca. 21%) consumption levels. They surmised that repeated consumption >30% is likely detrimental to plants and >45% removal is exceptionally high. We observed proportional OFTK >45% for browse species (Fig. 2) when moose in Units 20A and 20D were at relatively high density (>2/km^2). The poor nutritional condition indicated by low twinning rate of these populations (Fig. 5; also Boertje et al. 2007) suggests that such levels of browsing intensity have a negative effect on browse production. Despite uncertainty in the threshold of sustainable browse removal, the recent antlerless harvests in Units 20A and 20D intended to reduce relatively high moose densities and negative effects on the winter forage base seemed prudent regardless of whether proportional OFTK is considered at the level of study area or plant species.

We acknowledge that factors independent of change in moose density may influence estimates of browse metrics. We caution that our estimates of "apparent" production were for twigs above late winter snow depth in a limited number of plots, rather than a rigorous landscape estimate of total biomass production. The actual biomass available to moose might vary over time independent of moose abundance because of plant density in response to disturbance,

plant structural change since disturbance, compensatory growth over a life history of exposure to browsing, growing season limits to CAG (e.g., drought or insect defoliation), and competing herbivory by hares. Diet quality can multiply effects on intake rate to produce greater removal on better quality forages (White 1983, McArt et al. 2009). Study areas should remain large enough so that browse sampling allows inference at the population level and reduces annual variation in estimates of production and removal inherent at smaller scales (Ahlén 1975:111, 134–135, 165; Mackie 1976, Månsson et al. 2007). Managers wishing to monitor plant health should consider sampling designs focused on total production during the snow-free period and stratifying by vegetation type in addition to moose density. Finally, we urge others to replicate our evaluation of management actions in a more rigorous and balanced experimental design, recognizing the risk that public regulatory bodies can interrupt the duration or type of management "treatment" once baseline data are collected.

Our only case study of deep snow (107 cm in Unit 19D, 2009) was also our only case study of population increase. We do not know if Unit 19D would have had removal levels equally as high in 2009 had snow depth been <90 cm. Deep snow likely contributed to the increased 2009 browse removal in Unit 19D by concentrating moose and exacerbating the effect of increased density (K. Kellie, unpublished data). Testa (2001) noted that the proportional number of *S. alaxensis* twigs browsed on 2 important wintering areas in the Nelchina Basin of southcentral Alaska was 60–82% during winters with snow >70 cm compared with 12–35% during winters <70 cm. Collins (2002:11) further defined a positive relationship between snow depth and biomass removal for this population. Repeating surveys among winters of markedly different

snow depth for a relatively stable moose population would be instructive as to the effect of snow-depth on spatial distribution and degree of browse removal.

Twinning rates did not respond in an expected fashion during the intervening period between the end of management actions causing moose density to change and subsequent browse surveys (2–6 yr); presumably, immediate consequences to reproduction were small. We surmise that increased body weight of the youngest, non-reproductive cohorts may be a better short-term index to improved nutrition following reduced intraspecific competition. Lag in nutritional condition of wild ruminants has been documented following density reduction (Blood 1974, Albon et al. 1987, Boertje et al. 2007). Reduced twinning rate following prolonged high density might persist until enough more robust female calves born during periods of lower food competition enter the breeding population and affect the birth rate (e.g., Solberg et al. 2004). In 3 of our 4 study areas, estimates of apparent production also decreased, possibly reflecting a decline in per capita forage that could dampen reproductive responses (Solberg et al. 2012).

Our relevant case study in interior Alaska occurred in Unit 20A moose, where twinning rate took 12 years to increase despite a dramatic decline from peak abundance in the 1960s (Fig. 5 in Boertje et al. 2007). The lower twinning rate in the 1990s in Unit 20A, despite lower moose density than in the 1960s, may have been evidence of degraded range capacity from having moose at prolonged high density in the 1960s and less extensive wildfires after the 1960s (less forage per capita). Unfortunately, we do not have historic data on forage abundance or quality to evaluate this speculation. Time lag in reproductive response may differ among periods, or among populations, in part due to differences in vegetation recovery rate (Sand et al. 1996:242) that is

potentially influenced by negative effects on soil fertility from prolonged high biomass removal (Persson et al. 2005b).

Monitoring systems that quantify density-dependent responses of ungulates to their habitat as a correlate of population density have existed for decades (e.g., Aldous 1945), but few jurisdictions manage ungulate abundance primarily based on monitoring indices of habitat (e.g., Keigley and Fager 2006) or nutrition. DuBois (2008:388) first proposed use of twinning rate thresholds developed by Boertje et al. (2007) rather than a population objective to recommend management of moose population trend in Unit 20D. Our study demonstrated the value of browse biomass offtake for corroborating intended reductions in intraspecific competition and gauging relationship of moose abundance to carrying capacity at higher densities.

Offtake and twinning rate provide managers with objective means to recommend and monitor effectiveness of forage enhancement, or timely reduction in moose density through harvest across age and sex classes to reduce forage competition and avoid prolonged negative effects of high density (Boertje et al. 2007, Young and Boertje 2011). We urge managers and public regulatory bodies to utilize an empirical monitoring and decision framework for moose population management that incorporates measures of plant and animal condition in addition to population objectives. When reporting metrics on forage or animal condition, managers need to clearly identify that maintaining higher moose densities incurs an increased risk of strong negative feedback after severe winters (Gasaway et al. 1983, Boertje et al. 2009). When the public desires high moose densities, we encourage managers to discuss the risks associated with various management options and acceptable means for achieving proposed harvest

objectives (ADFG 2011, Young and Boertje 2011).

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