

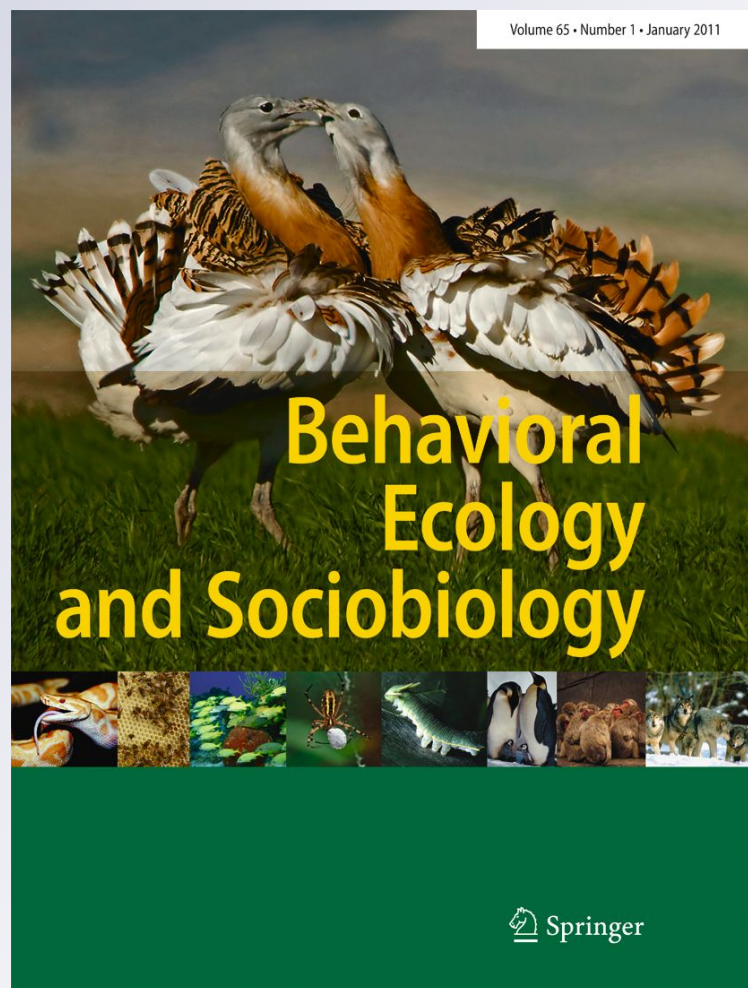
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Vocalizations by Alaskan moose: female incitation of male aggression

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Abstract Evidence of female fomentation of male–male aggression as a mechanism of mate choice is rare, especially in mammals. Female choice of mates in polygynous species may be masked by intense male competition or by males attempting to restrict female choice. We studied protest moans of female Alaskan moose *Alces alces gigas* in interior Alaska, USA, from 1987 to 1990, to determine if moans incited male–male aggression. Alaskan moose exhibit a mating system in which one dominant male (the harem master) herds, defends, courts, and attempts to mate with females in his harem. Protest moans were given by females only in response to courtship. We hypothesized that if protest moans were related to females reducing harassment and exercising mate choice, females should give protest moans more frequently when courted by small males and less often when courted by large males, and that rates of male–male

aggression would be elevated following protest moans. Harems were composed of one large male, with a mean of 4.4 females (median=3 females); 10% of 132 harems included ≥ 10 females. The temporal pattern of protest moans from late August through November was associated with, but tended to lag behind, mating behavior. The rate of protest moans given by females decreased with increasing size of males courting them. Male–male aggression was significantly less during periods without protest moans than during periods in which protest moans occurred. These results indicate that female moose gave protest moans to reduce harassment by smaller males, and assure a mating opportunity with the most dominant male. Such a subtle mechanism of indirect mate choice by females may occur in other vertebrates in which choice is limited by a mating system in which male–male combat and male dominance over females reduces opportunities for female choice. The importance of female choice may be undervalued in studies of sexual selection in mammals.

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Introduction

The theory of sexual selection was first advanced by Darwin (1871); choice of mates is widely recognized as an important component of that theory (Andersson and Simmons 2006). How female choice of mates evolved, however, has been the topic of spirited debate (Kokko et al. 2003 for review). Sexual conflict over mating may arise when there is an evolutionary difference in the interests of males and females (Parker 2006; Hunt et al. 2009 for reviews). Such conflicts relate to differences between sexes

in benefits of mating relative to its costs (Moore and Moore 1999; Parker 2006). Indeed, sexual selection by female choice often involves male–female conflicts of interest (Eberhard and Cordero 2003). Moreover, sexual conflict may be an important agent of evolutionary change (Rowe and Day 2006; Sullivan-Beckers and Cocroft 2010). Studies of mate choice in mammals, however, are less well-developed than for other taxa, because female choice can be masked by male competition or males attempting to limit choice by females (Clutton-Brock and McAuliffe 2009). Research on ungulates often focuses on male competition and neglects the role of female behavior in choice of mates (Bro-Jørgensen 2011).

Ungulates exhibit complex mating systems that affect patterns of female choice. Female Uganda kob *Adenota kob thomasi*, which mate on leks, select among males on territorial display grounds (Beuchner and Schloeth 1965; Leuthold 1966), but what attributes of males are being selected is uncertain. Female topi *Damaliscus lunatus* compete aggressively with one another for mating opportunities with males on central leks (Bro-Jørgensen 2002, 2003; Bro-Jørgensen and Durant 2003; Bro-Jørgensen 2008). In fallow deer *Dama dama*, male competition determines the dominance status of males, as well as influencing female choice (Balmford 1991; McElligott and Hayden 2000; McElligott et al. 2001; Ciuti and Apollonio 2011). In harem-mating red deer and North American elk *Cervus elaphus*, males attempt to limit female choice by actively herding females and excluding other males from harems via aggressive interactions (McCullough 1969; Clutton-Brock et al. 1979, 1982; Bowyer and Kitchen 1987), but females can exert some choice by electing whether to remain in a particular harem. Intrasexual interactions by males to settle dominance rank typically occur via male combat (McCullough 1969; Clutton-Brock et al. 1979; Mysterud et al. 2005; Mainguy and Côté 2008; Lovari et al. 2009), as well as visual displays (Jennings et al. 2002). A variety of cues exist to aid females in the selection of mates. Auditory signals (Bowyer and Kitchen 1987; Reby and McComb 2003; McElligott et al. 2006; Vannoni and McElligott 2007, 2009; Wyman et al. 2008) may be used by females to assess dominance status of males. Scent marking also can play a role in establishing male dominance and, similar to vocalizations, may provide a cue for females to assess male quality (Massei and Bowyer 1999; Stenström et al. 2000; Whittle et al. 2000). Female pronghorn *Antilocapra americana* choose mates based on their vigor or motor performance (Byers et al. 1994, 2010); females in territorial roe deer *Capreolus capreolus* make excursions to find alternative mates (Lovari et al. 2008). Female pronghorn also may sample male quality, but sometimes at a substantial cost (Byers et al. 2005, 2006). Clear evidence of mate choice also exists for

American bison *Bison bison*, both for female choice for large males (Bowyer et al. 2007), and for males selecting high-quality mates (Berger 1989). In these case studies, females are selecting from among the best males, because male–male aggression already has excluded low-quality males. Studies of females exerting mate choice by manipulating male–male aggression, however, are rare (Cox and Le Boeuf 1977; Byers et al. 1994).

Moose *Alces alces* have a circumpolar distribution and are closely associated with boreal forests throughout their range (Bowyer et al. 2003). These large herbivores are sexually dimorphic and polygynous; males are >40% heavier than females (Schwartz et al. 1987; Weckerly 1998). Their mating system typically is characterized as a tending-bond (sensu Hirth 1977), in which the sexes associate for a brief period that terminates following copulation, with males leaving in search of additional mates; moose are not territorial (Bowyer et al. 2003). In open areas, however, females typically form larger social groups compared with moose in more densely forested areas (Peek et al. 1974; Miquelle et al. 1992; Molvar and Bowyer 1994). Indeed, Alaskan moose *A. a. gigas* often form large social groups in open tundra or near the boreal forest-tundra ecotone, especially during the mating season (Molvar and Bowyer 1994; Bowyer et al. 2003). The primary mating season for moose peaks in late September and early October, and is extremely synchronous (Schwartz and Hundertmark 1993; Van Ballenberghe and Miquelle 1993, 1996). The increased degree of sociality exhibited by Alaskan moose compared with other subspecies likely has led to the evolution of harem mating, in which one dominant male (the harem master) herds and defends a group of females, and courts and attempts to mate with them as they come into estrus (Bowyer et al. 2003). Alaskan moose, however, herd females less vigorously (Van Ballenberghe and Miquelle 1993) than other species that mate in harems, such as North American elk (Bowyer and Kitchen 1987). Fierce combat among large males of near-equal dominance over possession of the harem occurs around the peak of the mating season (Peek et al. 1986; Van Ballenberghe and Miquelle 1993, 1996; Bowyer et al. 2003). A secondary mating period occurs in early November when moose no longer occur in harems but display a tending-bond mating system (Bowyer et al. 1994, 2003).

Social behavior of moose is well-documented (Van Ballenberghe and Miquelle 1993, 1996; Bowyer et al. 2003 for reviews); one lesser-known behavior, however, is moaning by females in response to courtship by males during the mating season. These vocalizations (hereafter termed protest moans) are plaintive, undulating calls of 3–5 s duration (Fig. 1). Protest moans by female moose differ from copulation calls of primates (Hauser 1993; Semple 1998; Maestripieri et al. 2005), because female moose



Fig. 1 A female Alaskan moose giving a protest moan in response to courtship by a small male, Denali National Park and Preserve, Alaska, USA. Photograph by Victor Van Ballenberghe

vocalize in response to courtship, not during, immediately before or after copulating. Protest moans may allow female moose to exert choice of mates by fomenting combat among males in a system where dominant males attempt to restrict female choice; these vocalizations also help reduce harassment of females by small males (Van Ballenberghe and Miquelle 1993, 1996; Bowyer et al. 2003). Female incitation of male–male combat has been documented in birds (Montgomerie and Thornhill 1989; Pizzari 2001), but is exceptionally rare among mammals (Cox and Le Boeuf 1977; Byers et al. 1994). Moreover, there is substantial interest in understanding how female choice might be influenced by competition among males (Wong and Candolin 2005; Clutton-Brock and McAuliffe 2009).

We observed moose during rut in a wilderness setting in interior Alaska, USA, where moose exhibit a harem mating system, to quantify temporal patterns and evaluate the social context in which protest moans were given by females. We also recorded information on male size and behavioral interactions relative to female vocalizations. We hypothesized that female moose employ protest moans to reduce harassment by small males and incite male–male competition, providing a pre-copulation mechanism for mate choice. We predicted that (1) females would emit protest moans more frequently when courted by small males than when courted by larger males; and (2) rates of male–male aggression would be elevated following protest moans.

Materials and methods

Study area

We observed moose in Denali National Park and Preserve (63°54' N, 149°50' W) in interior Alaska, USA. The study area encompassed approximately 300 km² in the eastern

portion of the Park within a broad valley between 700 and 1,200 m asl. This area is a pristine wilderness with one road along the valley floor, no trails, and limited recreational access. The area was bounded by the Alaska Mountain Range to the south and rugged foothills to the north (Bowyer et al. 1998, 1999). Vegetation consisted of a mix of open boreal forest of spruce *Picea glauca* and *Picea mariana* with a shrub understory of willow *Salix* spp. at higher elevations, resin birch *Betula glandulosa* and tundra at lower elevations, and willow thickets along riparian areas. The weather in the park during autumn is cool and snowy. Average temperatures during September, October, and November were 4.8°C, −5.1°C, and −12.6°C, respectively. Snow depths for those same months averaged 2.5, 7.6, and 20.3 cm, respectively.

A number of large carnivores occurred within the study area, including gray wolves *Canis lupus*, coyotes *C. latrans*, and grizzly bears *Ursus arctos*. Helicopter surveys indicated that approximately 150 moose inhabited the study area.

Observations of moose

We sampled behaviors of moose from late August through November 1987–1990. We accumulated >577 h of observations on moose when they were active (not bedded), and where observations of courtship and females giving protest moans were possible. We located groups of moose in the mating season (rut) during daylight hours by tracking radio-collared individuals ($n \sim 20$ each year) on foot or skis, and when weather permitted, by making opportunistic observations of groups while driving along the park road (~40 km). On average, we radio-collared 12 adult females and 8 males (6 large, 2 medium-sized) during each year of our study. Moose in Denali National Park and Preserve typically permitted investigators to approach to within 30–100 m apparently without being disturbed. Nonetheless, if moose exhibited alert (ears upright and directed toward the disturbance) or alarm (moving quickly away or running from the disturbance) behaviors toward investigators, we terminated collection of data on that group for the remainder of the day. Upon locating an undisturbed group (harem) of moose with at least one adult male and one adult female, we began sampling. If conditions were too windy to hear protest moans, we terminated observations. When distances were too great to hear male courtship grunts, we determined courtship bouts based on the body position of males, tongue-flicking, or other obvious courtship behaviors. Observations of moose typically involved three investigators, who recorded data with the unaided eye, 10× binoculars, or a 20–60× spotting scope. We recorded group size and composition, being sure that moose were not obscured by vegetation or topography, and that all

observers agreed on the total count of moose in each group. Groups of moose in this low-density population were seldom <100 m apart and typically were separated by several kilometers. The cohesive movements and activities of groups made it relatively easy to identify groups and determine group membership.

Once a group had been identified, the primary observer recorded general activities (standing, feeding, traveling, bedding) for each category of moose (large male, medium male, small male, yearling female, and adult female) by scanning at 15-min intervals (Altmann 1974). Thereafter, the primary observer used focal-group sampling, recording observations of the harem master and surrounding females. If the group was too large to watch all individuals simultaneously, we concentrated observations on the harem master and the females in his immediate vicinity. We recorded the amount of time that each moose was observed and noted their social behaviors. The secondary and tertiary observers watched for satellite males (typically medium and small males) on the periphery of the harem, and helped to locate females in the harem giving protest moans. We noted the behavioral context in which protest moans were given by females, and the size class and behaviors of nearby males that might have elicited those vocalizations; no moans were given in behavioral contexts other than during courtship by males. All procedures used in this research were approved by an Institutional Animal Care and Use Committee at the University of Alaska Fairbanks, and were in keeping with guidelines subsequently published by the American Society of Mammalogists for research on wild mammals (Sikes et al. 2011).

Evaluation of male size and behavior

We categorized adult males as large (antler spread of >155 cm; >7 years old), medium (100–155 cm; 3.5–6.5 years old), and small (<100 cm; 1.5–2.5 years old). Large males typically do not reach full antler growth until asymptotic body weight is attained at around 8 years of age (Stewart et al. 2000). Identifying categories of antler size was facilitated by having radio-collared males with known measurements of antler spread. We have substantial experience measuring and estimating antler size of Alaskan moose (Van Ballenberghe 1983; Bowyer et al. 2002; Schmidt et al. 2007), including relating age to antler spread (Stewart et al. 2000; Bowyer et al. 2001). Over the course of our study, 105 adult males were categorized during aerial surveys: 22% large; 27% medium; and 31% small.

Aggressive behaviors of males associated with rutting included antler thrashing, antler threats, a swaying gate, broadside displays, head held below the withers with the ears directed downward, rushing or charging toward an opponent, and fighting (Van Ballenberghe and Miquelle

1993, 1996; Bowyer et al. 2003 for descriptions). Other rut-related behaviors, such as sparring, were not included with more serious aggressive behaviors, because those behaviors were unlikely to resolve dominance relationships associated with mating and uncommon during the peak of rut (Bowyer et al. 2003). Courtship behaviors included a low grunting vocalization by males directed toward females, tongue flicking, flehmening, the male rubbing his chin across the rump of a female, mounting unsuccessfully, and mating (Van Ballenberghe and Miquelle 1993, 1996; Bowyer et al. 2003 for descriptions). We recorded a courtship bout whenever males directed those rut-related behaviors toward females.

Female protest moans

We recorded protest moans for females on an acts-per-active-hour per individual basis (Bowyer and Kitchen 1987; Rachlow and Bowyer 1994). Moose seldom engaged in social behavior when bedded. This method corrects for variation among observation periods in the proportion of time when moose were active. Under remote field conditions, investigators have limited control over when observation periods begin and end relative to the activities of study animals, and thus, what segment of the activity cycle of an animal is sampled. Acts-per-active hour help to control for those difficulties by excluding periods of inactivity in calculating rates of behavior.

We assessed the behavioral context in which protest moans occurred and their subsequent effects on male–male aggression by sub-setting our data into 518 15-min segments when $\geq 50\%$ of adult females were active (not bedded). We used only those intervals in which there had been no protest moans by any female in the previous 15 min; we then compared male–male aggression during 15-min segments within which no protest moan occurred with segments that included at least one protest moan, noting the size of the male (small, medium, large) that had elicited this vocalization by courting a particular female.

Statistical analyses

We used one-way analysis of variance (ANOVA) to test for differences in the rate at which female moose gave protest moans in relation of the size of males (Zar 1999). Pairwise post-hoc comparisons were conducted with Tukey's studentized range test (HSD). Data were rank-transformed to meet statistical assumptions of ANOVA (Conover and Iman 1981). We employed the chi-square test (Zar 1999) to evaluate differences in frequency of courtship by small, medium, and large males, and whether protest moans resulted in increases in male–male aggression. We combined data across years to have a sufficient sample size for

statistical analyses. Moreover, relatively few moose could be recognized as individuals, especially across years for those moose without radio collars. In addition, the composition of individuals in harems was not consistent during rut; we unquestionably sampled the same individuals more than once. Consequently, we lowered alpha to 0.02 to help compensate for inflating our sample size by potentially making more than one observation on the same individual (Bowyer et al. 2007).

Results

Group size and timing of female protest moans

Mean (\pm SD) number of females per harem was 4.4 (\pm 1.8) (median=3); >30% of 132 harems included \geq 5 females (Fig. 2). Harems included one large male and sometimes smaller “satellite” males near the periphery of female groups. Satellite males often approached harems and attempted to court females, but typically fled if challenged by the harem master.

The temporal pattern of 1,058 protest moans was associated with but lagged behind the timing of mating behavior. A marked increase in rate of protest moans by females ($n=851$) followed the peak in mating activities. A second increase occurred approximately 1 month later, when primiparous females that probably delayed estrus and other females that did not conceive during their first estrus likely recycled (Fig. 3). The timing of protest moans and two distinct peaks in their occurrence (Fig. 3) indicated that those vocalizations were rut-related and likely given by females during or close to their estrous period; protest moans increased and then waned with other rutting activities of moose.

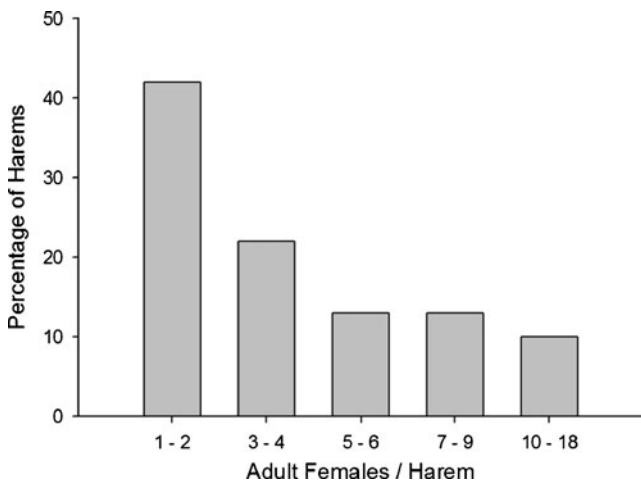


Fig. 2 Percentage of 132 harems of female moose, Denali National Park and Preserve, Alaska, USA, 1987–1990

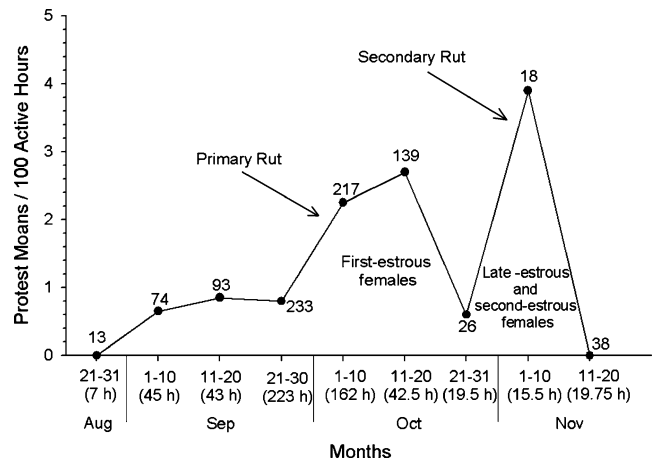


Fig. 3 Rates of protest moans ($n=1,058$) by adult female moose during the primary and secondary ruts, Denali National Park and Preserve, Alaska, USA, 1987–1990. Hours of observation of active moose are provided below dates in parentheses, and the number of separate observations of females giving moans are provided next to data points. Peak mating occurs in the last week of September and the first week of October

Frequency of protest moans in relation to male size

Females decreased rates of protest moans with increasing size of courting males (Fig. 4). We observed 98 bouts of courtship by large males, 21 by medium-sized males, and 29 by small males; this pattern was very different from that expected based on the proportion of males of different sizes in the population ($\chi^2=62.55$, $p<0.001$), and reflected harem masters limiting courtship by smaller males. Rate of protest moans during courtship bouts decreased with male

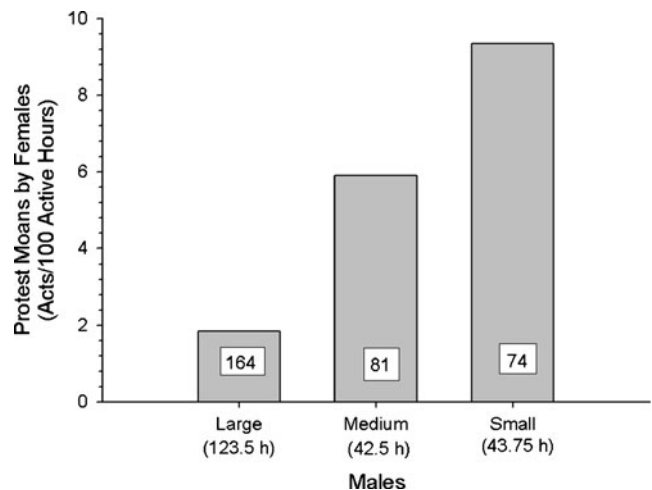


Fig. 4 Rates of protest moans by adult female moose in response to courtship by large (harem masters), medium, and small males, Denali National Park and Preserve, Alaska, USA, 1987–1990. Hours of observation of active moose are provided below each size class of male, and number of separate observations of males are provided inside bars

size ($F_{2, 148}=8.06$, $p=0.0005$), even though large males were involved in most courtship. Post-hoc comparisons with Tukey's HSD indicated that large males elicited protest moans from females less often than either medium- or small-sized males ($p=0.05$); rates of protest moans resulting from courtship by medium and small males did not differ (Fig. 4). Protest moans were given only in response to courtship by males. Relative to courtship by large males, rates of female protest moans increased threefold when courted by medium-sized males, and >4-fold when small males were courting females (Fig. 4). These results indicated that females protested courtship (and harassment) by medium and small-sized males most vigorously with this vocalization.

Female protest moans and male-male aggression

Protest moans stimulated male–male aggression. Aggressive interactions between males were >2 times as likely to occur in the 15-min interval that included protest moans than during periods without protest moans (Fig. 5; $\chi_1^2=60.77$, $p<0.001$).

Discussion

Adult female moose gave protest moans more often in response to courtship by small- and medium-sized males than by large males, even though large males engaged in more courtship bouts. This outcome indicates that females were attempting to affect mating opportunities for smaller males by

eliciting aggression by large males, although they also protested courtship by large males at a low rate. Indeed, protest moans sometimes resulted in a test of the dominance status of the harem master. During our study, protest moans were given only in response to courtship by males. Subsequently, however, one author (Van Ballenberghe) once observed protest moans given in response to the approach of another female. Given our large sample size, the use of protest moans in this other context is rare.

Protest moans undoubtedly helped reduce harassment of females by smaller males. Female mortality from male harassment has been demonstrated in another polygynous ungulate during rut (Réale et al. 1996). The lag in protest moans behind peak mating activities of moose might represent increased courtship by smaller males, which elicited more protest moans from females. We further hypothesize that a reduction in number of estrous females during the second rutting peak may have made harem mating unprofitable for males, and resulted in the adoption of a tending-bond mating system. Indeed, degree of female aggregation is an important component in determining ungulate mating systems (Pérez-González et al. 2010). We recorded a second large peak in rates of protest moans by females during early November, when some females were likely undergoing a late or second estrous cycle. Young females delay ovulation compared with older ones (Garel et al. 2009). A tending-bond mating system may allow more harassment of females by smaller males than does harem mating; in tending bonds, the dominant male defends a single female at a time, allowing for courtship of other females by smaller males while the dominant male is preoccupied. We also hypothesize that the second peak in protest moans was higher than during the primary rut because smaller males were more actively involved in courtship, during a time when dominant males were exhausted from earlier rutting activities. Rutting male moose cease feeding for about 18 days during the peak of rut (Miquelle 1990), and may lose 12–18% of their body weight during that period (Schwartz et al. 1987). Among ungulates, smaller males are less likely to compete successfully for mates with larger males, and paternity is strongly skewed toward prime-age males (Maher and Byers 1987; Pemberton et al. 1992; Coltman et al. 2002). Nevertheless, smaller males have a greater likelihood of siring offspring when dominant males are exhausted (Preston et al. 2001; Mysterud et al. 2008), and this outcome could explain why smaller males begin to show more interest in mating activities later in rut than do dominant males (Mysterud et al. 2005).

Male–male aggression occurred more often in sampling periods that included protest moans than those that did not contain moans. Thus, females incited aggressive behavior among males to gain an element of mate choice in a mating

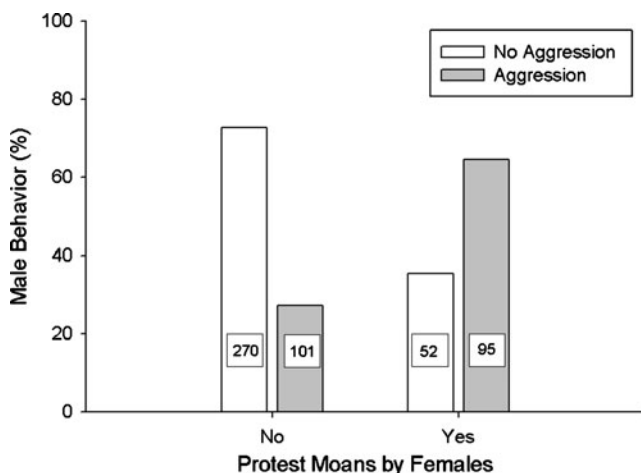


Fig. 5 Percentage of behavior by adult male moose that was aggressive or not aggressive during 15-min intervals without protest moans, and 15-min intervals with protest moans by females, when $\geq 50\%$ of females in the harem were active (*not bedded*), Denali National Park and Preserve, Alaska, USA, 1987–1990. Number of 15-min sample intervals is provided *inside bars*

system in which male–male competition limited female choice. The behavior of females reinforced the existing system of the dominant males mating most often, yet females obtained some measure of mate choice in doing so. This behavior is an example of indirect mate choice (Wiley and Poston 1996) wherein females help set conditions for competition among males, and by doing so, increase their likelihood of mating with a successful competitor.

We encountered several challenges in conducting our research on moose. The remote setting, rugged terrain, harsh weather conditions, shortened day lengths, and low density of moose reduced sample sizes below what we initially envisioned. We were forced to combine years to have adequate sample sizes for statistical analyses. Nonetheless, we obtained robust patterns of females giving protest moans more often in response to smaller than larger males, and those vocalizations fomenting aggression among males—we do not believe that combining years introduced a strong bias into our data. We could not consistently recognize individual moose that were not radio-collared and likely sampled individuals more than once. Consequently, we lowered alpha to help correct for inflating sample size and reduce the probability of making a type I error. Moreover, about 13% of moose in this subpopulation were radio-collared, which raises the possibility that using those moose to locate harems for behavioral observation somehow biased our results. We attempted to overcome this potential problem by opportunistically sampling groups of moose we encountered while traveling along the park road—depending upon habitat and weather conditions, moose could be surveyed at distances of ≤ 500 m. In addition, we acknowledge that the interval we selected for evaluating effects of protest moans on male aggression was somewhat arbitrary—a time scale >15 min may have yielded different results. We selected this particular interval because it matched our scan sampling of activity patterns, and for the reason that a longer temporal scale would have drastically reduced the number of intervals without protest moans, thereby making our comparison problematic. Moreover, this relatively short interval helped to assure that male–male aggression we observed was associated with a protest moan rather than being caused by other factors. In addition, if a protest moan occurred near the end of the 15-min interval, the time during which male–male aggression could be observed was diminished. This potential bias, however, makes our analysis of effects of protest moans on male competition conservative—we still detected a strong pattern of male–male aggression associated with protest moans by females.

Unequivocal evidence of females fomenting combat among males to exercise mate choice is rare among vertebrates (Cox and Le Boeuf 1977; Montgomerie and Thornhill 1989; Byers et al. 1994; Pizzari 2001). Although

courtship chases in some ungulates may result in male–male aggression (Cox and Le Boeuf 1977 for review), whether this behavior allows females to discriminate among potential mates remains uncertain. Moose are an excellent model for understanding female choice; these large herbivores are sexually dimorphic, highly polygynous, and males provide no investment in offspring except for inseminating females (Bowyer et al. 2003). Under these circumstances, females would be expected to choose mates based on phenotypic characteristics. In addition, forced copulation is uncommon in moose, and females typically accept copulation from only one male (Bowyer et al. 2003), behaviors that indicate females can be choosy. Moreover, antler size, symmetry, and age are correlated in moose (Bowyer et al. 2001), and males do not fully invest in antler growth until asymptotic body weight is reached (Stewart et al. 2000), a pattern typical of cervids (Monteith et al. 2009). Older males with large antlers typically mate more often than smaller conspecifics (Clutton-Brock et al. 1982; Bowyer 1986; Ciuti and Apollonio 2011). Size of antlers also reflects sperm production and quality (Malo et al. 2005). Adult male moose scent-urinate in rutting pits, which attracts females to the pit, and, like antlers, may be an honest advertisement of male quality on which females could base decisions about selecting a fit mate (Whittle et al. 2000). Females also might exhibit some choice of mates by selecting which rutting group to join, or waiting for a turnover of harem masters as a result of male combat.

Another aspect of the life-history characteristics of females also may limit their choice of mates. Female moose give birth in an extremely synchronized manner in late May, with little interannual variability (Bowyer et al. 1998). At far northern latitudes, the growing season is exceedingly restricted, and there is a limited time for young to garner resources necessary to survive harsh winter conditions (Rachlow and Bowyer 1991; Bowyer et al. 1998, 1999). Consequently, maternal females must time parturition so that neonates do not succumb to severe weather in early spring, but are born early enough to acquire the necessary resources to survive winter (Rachlow and Bowyer 1991; Bowyer et al. 1998). Females can adjust gestation length (Rachlow and Bowyer 1991; Berger 1992; Schwartz and Hundertmark 1993), but late-born young tend to be smaller and suffer greater mortality than their early born counterparts (Keech et al. 2000). Females that exercise mate choice in the primary rut and choose not to mate with the harem master (i.e., wait for another male), may risk delaying conception until early November. Although moose can shorten the length of gestation by several weeks (Schwartz and Hundertmark 1993), a delay in conception would still result in a late-born neonate that was small and subject to a high risk of mortality (Keech et al. 2000).

We present evidence of indirect mate choice by female moose, restricted by intense intrasexual competition when males attempt to limit female choice via dominance interactions with other males. Females use protest moans to foment male competition and reduce harassment by small males. Such behavior is rare and only has been documented for one other large mammal, the elephant seal *Mirounga angustirostris* (Cox and Le Boeuf 1977), although female pronghorn also incite male–male aggression by means other than vocalizations (Byers et al. 1994). Other recent evidence of female mate choice in large, polygynous mammals (Bro-Jørgensen 2002; Bowyer et al. 2007; Lovari et al. 2008; Byers et al. 2010; Ciuti and Apollonio 2011) indicates that this phenomenon may be more widespread in polygynous mammals than previously thought, and likely plays a critical role in the evolution of their mating systems.

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