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Male size and alternative mating tactics in white-tailed deer and mule deer

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Within populations, individual males adopt different courtship tactics due to differences in their competitive ability, which may vary depending on the animal's age and size. To test the hypothesis that mule deer (*Odocoileus hemionus)* and white-tailed deer (*O. virginianus*) males vary their courtship behavior based on their size, we conducted focal observations of 144 mule deer and 85 white-tailed males that varied in size, at a large grassland site in southern Alberta. The smallest mule deer males devoted more time to feeding, were less likely to engage in late-stage courtship than larger males and were less likely to move among female groups. Other males, including small white-tailed males, appeared to use a roving strategy to search for estrous females in different groups, which is consistent with recent research on male movements. Both medium and large males increased the time they spent in one-male groups, and specifically isolated pairs, as courtship advanced, presumably to reduce competition with other males. However, this trend was most pronounced for medium mule deer males, and for all size classes of white-tailed deer. In contrast, large mule deer males spent a similar proportion of time tending females in all group types. Our results identified potential size-dependent tactics for mule deer males. In contrast, white-tailed males of all sizes appeared to rely on a tactic of finding and tending estrous females in isolation from other males.

Key words: alternative tactics, body size, cervids, reproduction, reproductive effort, scramble competition

Biologists traditionally have described species as having a single breeding system or mating tactic. This implied that individuals in a population exhibit the same courtship behavior. However, courtship behavior varies widely among individuals (Taborsky et al. 2008), with individuals modifying their behavior to maximize reproductive success (Koenig et al. 1992; Sinervo and Lively 1996). Changes in reproductive behavior often are driven by changes in competitive ability, which for males often is related to age or body size (Mysterud et al. 2004; Isvaran 2005; Pelletier et al. 2006; Bowyer et al. 2020).

Prime-aged males account for most of the breeding success in species where dominant males defend resources sought by females or groups of females (McElligott et al. 2001; Mysterud et al. 2004; Wade and Shuster 2004). Nonetheless, smaller males may find opportunities that enable them to find mates, often while avoiding direct confrontation. For example, larger male grey seals (*Halichoerus grypus*) and Southern elephant seals (*Mirounga leonina*) form harems on shore, whereas smaller males pair breed with females in the water offshore (Ambs et al. 1999; Fabiani et al. 2004). More dominant fallow deer males defend individual or grouped (lek) territories where females gather, with less competitive males finding breeding opportunities by following female groups or occupying satellite positions near these territories (Apollonio et al. 1992; Moore et al. 1995).

When females form small groups or are dispersed across the landscape, both large and small males may engage in scramble competition as they search for or guard individual females entering estrus (Lane et al. 2009; Foley et al. 2015). Red squirrel (*Tamiasciurus hudsonicus*) females are highly territorial, and males must use their time efficiently to move among female territories to maximize their reproductive success (Lane et al. 2009). Like red squirrels, bighorn sheep (*Ovis canadensis*) only court one female at a time, possibly because female bighorn sheep form small groups during the reproductive season. This social organization forces males to rove among groups searching for estrous females (Pelletier 2005). Once paired with a female, the largest most competitive males rely mostly on tending one estrous female at a time, with a successful male pairing with multiple females over the breeding season (Hogg 1984; Hogg and Forbes 1997).

Because a large tending male focuses his attention on one female, he is unable to monopolize reproductive access to multiple females at any given time (Coltman et al. 1999; Preston et al. 2003; Sorin 2004). In bighorn sheep, subordinate rams frequently turn to two alternative mating tactics. One is blocking, in which a male isolates a female until she enters estrus and is willing to mate (Hogg 1984). The other more common and successful alternative tactic of small bighorn rams is coursing (Hogg and Forbes 1997; Pelletier 2005; Pelletier et al. 2006). Coursing rams follow tending pairs, aggressively intercepting the pair and initiating combat with the tending ram to gain temporary access to the estrous female (Hogg 1984).

In white-tailed deer (*Odocoileus virginianus*), small younger males sire 25–40% of offspring in some populations (Sorin 2004; DeYoung et al. 2009; Turner et al. 2016; Newbolt et al. 2017). Although unreported, this same pattern may occur in mule deer (*O. hemionus*) because the two species are closely related (Cronin 1991), sympatric in parts of their range (Brunjes et al. 2006) and, most importantly, share similar courtship behavior (Hirth 1977; Kucera 1978; Geist 1981; Airst and Lingle 2019). Observational studies indicate that white-tailed deer and mule deer males sequentially investigate multiple females, after which a male will try to tend or guard the female throughout her estrus (Hirth 1977; Kucera 1978; Geist 1981; Airst and Lingle 2019). As with bighorn sheep, tending seems maladaptive for small white-tailed and mule deer males, because they may not be able to attract or defend females successfully against larger males (Hirth 1977; Geist 1981). Small males may instead opt for alternative tactics. Blocking has been reported as a rare behavior in mule deer but has not been described in white-tailed deer (Geist 1981; Airst and Lingle 2019). Coursing has not been reported in these or other cervids, perhaps because coursing is potentially more dangerous for cervids, due to their piercing rather than concussive weapons (Hogg 1984). Instead, smaller males of some cervid species occasionally use sneaky or opportunistic tactics to pair with females while avoiding confrontations with larger males (Pemberton et al. 1992; Holand et al. 2012).

Alternative tactics often involve variation in the spatial and social context in which reproduction occurs, not only in the specific form of a male's interactions with a female. Young adult (2-year old) white-tailed males travel distances similar to those covered by older males, presumably searching for females and reproductive opportunities (Foley et al. 2015). These young males lost a similar proportion of their body mass as older males over the reproductive season, suggesting a similar energetic investment in reproduction (Foley et al. 2018). Further, they sired 16% of offspring. In contrast to adults, yearling white-tailed males during the rut did not travel long distances (Foley et al. 2015) or lose body mass (Foley et al. 2018). Even so, yearling males fathered 19% of offspring, suggesting they may find breeding opportunities while adopting a residency strategy of staying in areas or groups with specific females until the females enter estrus (Sorin 2004; Foley et al. 2015), before a larger male displaces them. If occupying the same group as another male, a smaller male might simply court different females within the same group (concurrent courtship) or wait until larger males tire, tactics reported for bison and reindeer that form large multi male-multi female groups (Wolff 1998; Holand et al. 2012). Concurrent courtship also is documented in mule deer but not in white-tailed deer (Airst and Lingle 2019).

Foley et al. (2015) used GPS collars to track male movement patterns over space and integrated these results with data on energetic costs of reproduction obtained by analysis of harvested animals (Foley et al. 2018). The purpose of the present paper is to extend our understanding of how body size influences male reproductive strategies by using observations of free-ranging deer to document size-related variation in courtship effort and tactics. We aimed to determine (1) how much time (effort) males of different sizes spend investigating or paired with females; (2) whether the social groups in which courtship occurs differ for the different size classes; and (3) whether the specific tactics males use to court females, e.g., tending or blocking, depend on the male's size.

We hypothesized that males vary their courtship behavior based on their size due to differences in their competitive abilities (Table 1). First, we predicted that larger males would devote more time, and therefore energy, to courtship (Table 1: Prediction 1, courtship effort), because they have the body reserves to support energetically demanding activities (Yoccoz et al. 2002)

Table 1.——Predictions associated with the hypothesis that males vary their courtship behavior based on their size due to differences in their competitive abilities. For specific forms of alternative courtship tactics included under Predictions 2 and 3, "Less" or "More" refers to "less likely" or "more likely" when compared with other size classes of males.

Predictions	Small	Medium	Large
P1: Courtship effort: Larger males will devote more time (energy) to reproduction.			
P1A: Time spent courting female(s)	Least	Intermediate	Most
P1B: Time spent foraging	Most	Intermediate	Least
P2: Social context			
P2A: Isolated pairs	More	Intermediate	Less
P2B: Group residency	More	Less	Less
P2C: Opportunistic concurrent courtship	Present	Present	NA
P3: Specific form of courtship. Smaller (small and medium) males are more likely than large males to use alternative mating tactics			
P3A: Tending	Least	Intermediate	Most
P3B: Blocking	Less	More	Less

along with a high probability of success. This effort would be reflected by larger males spending more time courting females (P1A) and less time eating (P1B) than smaller males.

Second, we predicted that smaller (small and medium) males would vary the social or spatial context in which they court females to reduce competition with other males (Table 1: Prediction 2, social context). We considered three forms this could take. We predicted smaller males to be more likely to court females in isolation from other males to avoid competition with other males (P2A, isolated pairs). Conversely, the very smallest males might forego active mate searching and instead adopt a residency tactic of remaining in areas or groups with specific females (P2B, group residency), which may enable them to maximize food intake and minimize costs of active mate searching while occasionally getting first access to an estrous female (Sorin 2004; Foley et al. 2015, 2018). Small resident males, and larger males that occupy the same group as a tending pair, might avoid competition by courting females only when a larger male is preoccupied by courting another female (P2C, opportunistic concurrent courtship).

Third, we predicted that the specific form of courtship interaction with females would vary with male size (Table 1: Prediction 3, courtship tactics). The largest males should be more likely to use a tending tactic during late-stage courtship (P3A, tending), because their superior competitive ability should increase their ability to attract females and repel rivals. Even though the largest males may at times adopt alternative mating tactics in response to competition from their rivals (Hogg 1984; Hogg and Forbes 1997), smaller males face stiffer competition and would, therefore, be more likely to adopt alternative courtship tactics. Regarding a male's specific interactions with females, we predicted that medium males would be more likely than small males to use blocking to sequester and court females; blocking requires the ability to dominate females, which smaller males may lack (P3B, blocking).

Materials and Methods

Study site and subjects.—Observations were carried out on the McIntyre Ranch, a 225-km^2 private cattle ranch in southern Alberta (49°N, 112°W, elevation 1,080–1,380 m) from 1 November to 15 December, in 2014 and 2015. This corresponded to the breeding season for both species. The site is dominated by fescue (*Festuca campestris*) grassland, with topography representing the greatest source of habitat variation (Lingle 2000, 2002). Coyotes (*Canis latrans*) were the main predators of deer during this study and recreational hunting was not permitted on the ranch. Juvenile deer at this location typically experience high mortality from coyote predation, which appears to be followed by high adult survival (Lingle et al. 2008).

Population demography.—Population surveys undertaken during this study (Airst and Lingle 2019) showed that the white-tailed deer population was more female biased than the mule deer population (male: female: white-tailed = 1:2.6, mule deer = 1:1.6). Further, a greater proportion of white-tailed deer groups were all female, and mixed sex groups were larger for mule deer, containing both more males and females (Airst and Lingle 2019). The mule deer male population included 7% yearlings, 18% small males, 45% medium males, and 29% large males (Airst 2017). The white-tailed male population included 5% yearlings, 12% small males, 48% medium males, and 35% large males (Airst 2017).

Male size categories.—Body size and antler size were used to assign individual adult (≥2-year old) males to a size category (Table 2; Supplementary Data SD1). These traits were chosen because they independently contribute to an individual's investment in reproduction (Newbolt et al. 2017). Yearling males rarely were observed courting. Because of this and the shortness of the observation season, we focused on adult males. Nevertheless, the presence of yearling males in groups still was recorded when they were in a group with a focal subject.

We relied on a male's size to draw conclusions from the results of this study, and only considered how these categories may correspond with age when comparing our results with those of other studies in the discussion. Assessing the age of adult cervids is challenging, regardless of whether the animals are active or sedated. Studies that categorized age of sedated animals have traditionally relied on the "tooth development and wear" method (Severinghaus 1949). This method has been found to be useful only to distinguish yearlings with a relatively high probability (~80%) from older males (Gee et al. 2002; Storm et al. 2014). Researchers attempt to minimize errors by distinguishing males into three age classes (yearling, 2-year old, and ≥3-year old—e.g., Sorin 2004; Foley et al. 2015).

Table 2.——Male size categories used to distinguish yearling, small, medium, and large white-tailed deer and mule deer at the McIntyre Ranch, AB.

Size	Body characteristics	Antler characteristics
Yearling	Same height as a female, but shorter body length so that the male's body length appears equal to its height	Highly immature antlers; very thin diameter; having a single antler spike and occasionally one fork; antlers nearly vertical
Small	Adult proportions; similar or smaller body size to a female	Immature antlers; thin diameter; short beam; antlers no wider than head; reduced number of tines (2–3)
Medium	Adult proportions; body larger than a female; chest and rump noticeably begin to thicken	Mature antlers; moderate diameter and overall length; antlers typically no wider than ears; each typically with 3 or 4 tines (including main beam for white-tailed deer)
Large	Adult proportion; body larger and broader than female; thick neck, deep chest, rump and forelimbs thickened	Mature antlers; thick diameter; long main beam (white-tailed deer) or overall height (mule deer); antlers wider than ears; each typically having ≥4 tines and longer tines

Another approach that wildlife managers use is "aging on the hoof," which uses body and antler characteristics to estimate the age of live and active animals (Hellickson et al 2008). Recent attempts to validate these methods revealed that trained biologists using either method—tooth development and wear or aging on the hoof—tend to overestimate the age of young males (e.g., some 2-year old males are identified as 3 years or older) and to underestimate the age of older males (Gee et al. 2002; Storm et al. 2014). Further, these studies reveal that body size, antler size, and tooth wear vary considerably within an age group, even for individuals from the same population. We assessed body and antler characteristics to place males into size, not age categories. However, the specific direction of errors reported by these validation studies and the large proportion of males in this population classified as medium and large (74% of mule deer, 83% of white-tailed—Airst 2017) suggests that a large proportion of males in the populations we studied were 3 years or older.

Focal observations.—The open grassland and varied topography enabled long-distance observations of animals from vantage points throughout the study site. We used high-powered optics (Swarovski 15 × 56 binoculars and Swarovski 20-60 × 80 mm spotting scopes) in addition to Vortex 8 × 42 binoculars to observe animals from 200 m to 2000 m (median distance = 750 m). A topographic map was used to approximate the distance between the subject and observer. Most observations were made after walking to a vantage point, but 11% were made from a motor vehicle.

We conducted 229 focal observations of white-tailed and mule deer males during the 2014 and 2015 breeding seasons (2014: 46 white-tailed, 67 mule deer; 2015: 39 white-tailed, 77 mule deer). The maximum observation time during the first season was 1 h, which was increased to 2 h during the second season. By increasing the observation time, we were able to better assess courtship intensity. We randomly sampled adult males that varied in size to capture behavioral variation that may occur within each species and size category. This meant that we sampled males as they were encountered; when we encountered multiple males at the same time, we tried to sample an equal number of males from each species and size class.

Several precautions were taken to prevent unintentional repeated sampling of focal subjects. First, within the 225 km^2 ranch, we rotated among eight main areas (each about 8–16 km^2) that were delineated by topographical features (e.g., river valleys, slope systems). Second, we recorded the focal subject's physical features, and only sampled individuals that could be distinguished from previously sampled individuals from the same area (see also Sánchez-Prieto 2004). Physical features of each male sampled included body size, species, antler characteristics (width, thickness, number, and configuration of antler tines), facial features such as coloration of nose and face, damage to the ear pinnae, shape and coloration of rump patch and tail, and other unique features. Individual identities only were considered accurate within seasons. Photographs were taken of each focal deer using a smart phone attached to the

spotting scope using an adapter (Phone Skope, product code: C3-049-A, Phone Skope, Beaver, Utah).

The primary observer used a 1/0 (presence/absence) recording rule to identify whether the focal male engaged in courtship during each 1-min observation interval (see Airst and Lingle 2019 for details), and also recorded the approximate distance (≤ 5, 10, 20, 50, and 100 m) between the subject and the nearest female and nearest male at the beginning of each minute. Data gathered during early-stage and late-stage courtship were analyzed separately. Early-stage courtship (also referred to as investigation) involved a male interacting with a female for a short duration (normally <5 min), typically until the female urinates and the male flehmen tests her urine, after which he moves to other females. We defined late-stage courtship as an interaction in which a male devoted at least 20 min of his attention to one female. In both stages of courtship males typically use a low stretch approach (a male approaches female with head in line or below body and with the neck extended forward—Hirth 1977; Kucera 1978; Geist 1981). See Airst and Lingle (2019) for a full list and description of courtship behaviors observed.

A group was defined as including every individual within approximately 50 m of the focal subject. Groups were placed into one of six categories: lone male, bachelor group (multi male–no female), isolated pair (one male–one female), one male-multi female, multi male-one female, and multi male-multi female. A second observer scanned the group once every 5 min during the observation period to update group composition. This person kept track of the identity of other (non-focal) males within the same group during each focal observation. Between scans, this person recorded the presence/absence (1/0) of courtship by each male within 50 m of the focal subject during the 5-min time interval, so that we could document concurrent courtship by different males in the group.

Ethical note.—Research conformed to ASM guidelines (Sikes et al. 2016) and adhered to the Canadian Council on Animal Care (CCAC) Guidelines (University of Winnipeg Animal Care Committee protocol RS172).

Data analysis.—We analyzed focal observations that lasted more than 30 min when determining the proportion of time each male spent in each group type. We excluded periods when deer appeared to react to predators or humans. Even with precautions taken to prevent repeated sampling of individuals during focal sampling, some individuals may have been unintentionally included more than once within the same year or in different years, which could have created non-independent samples (Bowyer et al. 2003). We therefore chose techniques that used empirical standard error such as generalized estimating equations (GEE) and bootstrapped bias-corrected and accelerated confidence intervals (BCa CI) to correct for potential variance underestimates (Burnham and Anderson 2002) and Type I error increases (Clifford et al. 1989). Analyses were undertaken using R version 3.3.2 (R Core Team 2019).

First, we tested the courtship effort predictions that larger males devoted more time to courting (Table 1: P1A) and less time to eating (P1B). Courtship was separated into early-stage

courtship and late-stage courtship. We used a general linear model (GLM) with a Poisson distribution to compare the rate (minutes/duration of observation, which is equivalent to the proportion of observation time devoted to courtship) of early-stage courtship by different size classes of males. The count of the total number of time intervals (minutes) during which each subject investigated a female was the response variable, with the log of the duration of the observation period entered as an offset (a constant) to control for variable observation length (as suggested by Gardner et al. 1995).

Only a small subset of males engaged in late-stage courtship during a focal observation, and males that did, usually spent most of their time in this activity, resulting in a binomial distribution. We therefore used a GLM with a binomial distribution to examine the likelihood of late-stage courtship (yes or no). We used a GLM with a Gaussian distribution to compare logged foraging rates for the three size classes of males.

We then tested three ways in which smaller less competitive males could vary the social or spatial context in which they searched for or courted females to reduce competition with other males (Table 1: Prediction 2, social context). To determine whether smaller males were more likely to form isolated pairs when courting females (P2A, isolated pairs), we tested whether small, medium, and large, males courted females in the same group types they occupied during their general activities. We used a GEE with a Poisson distribution and an exchangeable correlation structure to compare the time (minutes/duration of focal observation) a subject spent in each male–female group type, analyzing males of each size class within a species separately. When analyzing a male's group type during his overall activities (non-courtship, early-stage and late-stage courtship combined), we entered the total number of minutes the subject male spent in each group type during the focal observation as the response variable, included the log of the duration of the observation as an offset to control for variable focal length (as per Gardner et al. 1995), and included the male's identity as a random effect. We ran the same type of analyses for early-stage and for late-stage courtship, with the response variables being the number of minutes that the male engaged in the specific stage of courtship. We restricted the analyses of courtship to individuals who spent at least one minute in the stage of courtship we were examining. These analyses were done using the R package "geepack" (Højsgaard et al. 2019).

To assess whether a male's size predicted his likelihood of staying in a single group (P2B, residency) or leaving to find a new group (roving), we used a binomial GLM to compare the proportion of focal observations in which each size of male remained in a single group for the entire observation period (yes = 1, no = 0). We defined a group change as the subject moving >100 m from their original group or moving into a new group in which all members were >50 m from the original group. In this analysis, we used a 30-min subset of each focal observation to control for observation length, because movement would be more likely with longer observations. To form the 30-min subset, we randomly selected six 5-min observation intervals (group composition was updated each

5 min) from a focal observation. We excluded periods of time when males tended females and times when males moved to new groups after getting displaced from their original group by another male. When males tend females, they usually are not searching for another female; changes in groups, therefore, may be driven by the female's behavior. A male's decision to join a new group after being displaced from one group by another male may be driven by the dominance interaction and not by mate search activity.

We then tested the prediction that small and medium males that were in the presence of a larger male would be more likely to court a female when the larger male was preoccupied by courting a female than at times when the larger male was not courting (Table 1: P2C, opportunistic concurrent courtship). We used Mann–Whitney U tests to compare the proportion of time the smaller male courted a female in these two types of situations, running a separate analysis on each type of dyad: small versus medium males, small versus large males, and medium versus large males. In each dyad, the focal subject may have been either the smaller or the larger male. Data used for this analysis came from the 5-min observation of the second observer and was restricted to periods during which the subject was in a multi male-multi female group.

We used the proportion of a male's total time devoted to different activities (courtship, feeding, overall activities) when calculating descriptive statistics, mean differences for effect sizes, and to illustrate data (Figs. 1–3). Descriptive statistics are reported as the $\bar{X}$ [95% CI]. We relied on the inferential models described earlier (e.g., GEE, GLM) to identify differences between groups (α = 0.05) following a significant groupwise result. Wald chi-square (binomial and Poisson GLM) or F-score (GLM, foraging only) and P-values were reported for all groupwise tests. These were calculated using the "car" package in R (Fox et al. 2020). We use the mean difference ($\Delta\bar{X}$ [95% CI]) between groups to represent the effect size for most analyses, with Odds Ratios [95% CI of OR] for binomial GLM. We used BCa CI to calculate confidence intervals and means, because this method is capable of handling skewed distributions and identifying CI that are asymmetrical around the mean. BCa CIs were calculated using the R package "boot" with 5,000 iterations (Ripley and Canty 2019). Effect sizes were calculated using the R package "dabestr" (Ho 2020).

Due to the lack of variation in specific courtship tactics, we present descriptive data to test Prediction 3 (courtship tactics), which suggests that larger males of both species would be more likely to use tending during late-stage courtship (P3A) and that medium-sized males of both species would be more likely to use the alternative tactic of blocking during late-stage courtship (P3B).

RESULTS

Prediction 1, Courtship effort.—Size affected the time mule deer males devoted to early-stage courtship and their likelihood of late-stage courtship. Small mule deer males spent a larger proportion of their time in early-stage courtship than medium or large males (Fig. 1A; Poisson GLM: χ^2 = 55.521, 2 *d.f.*,
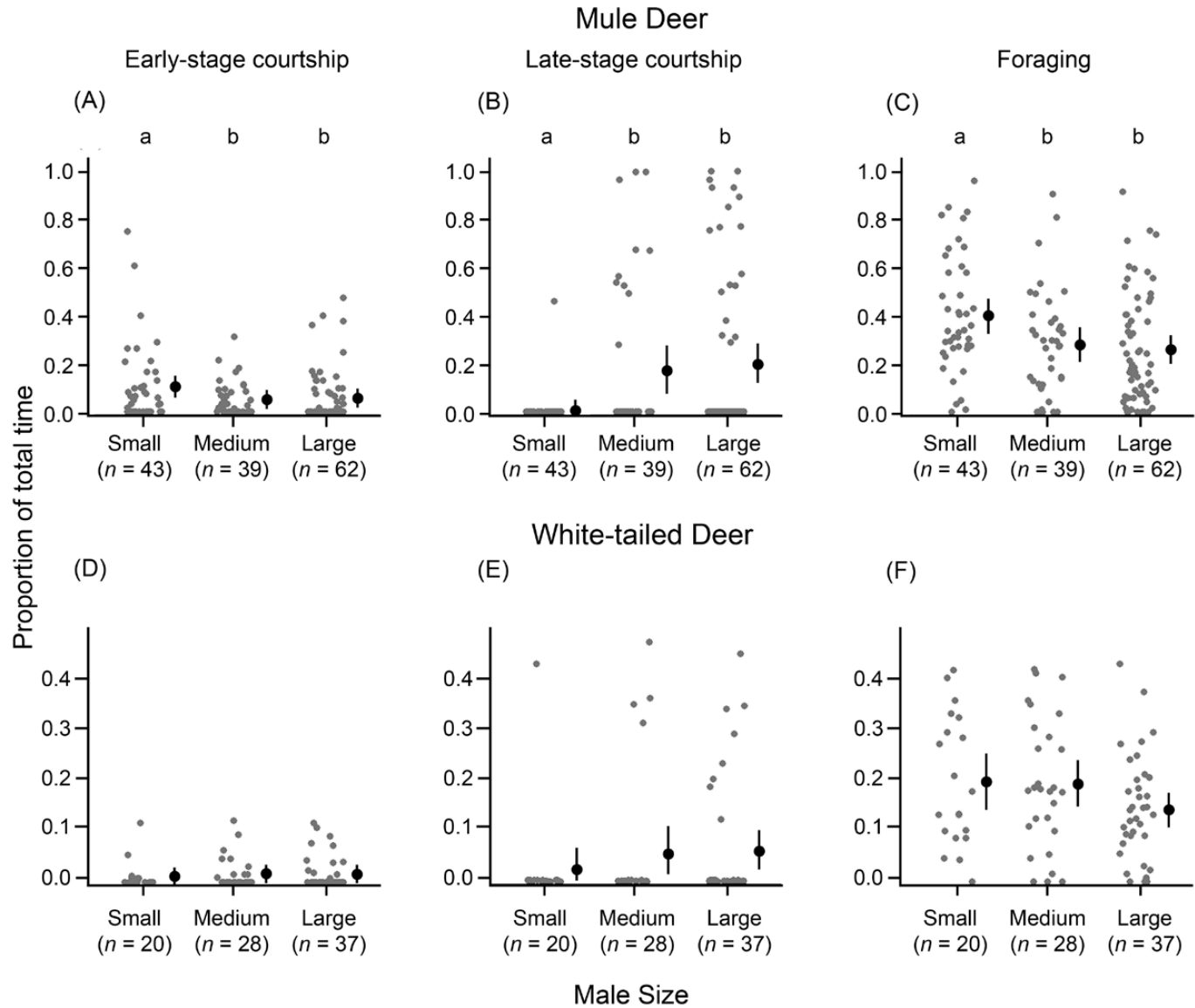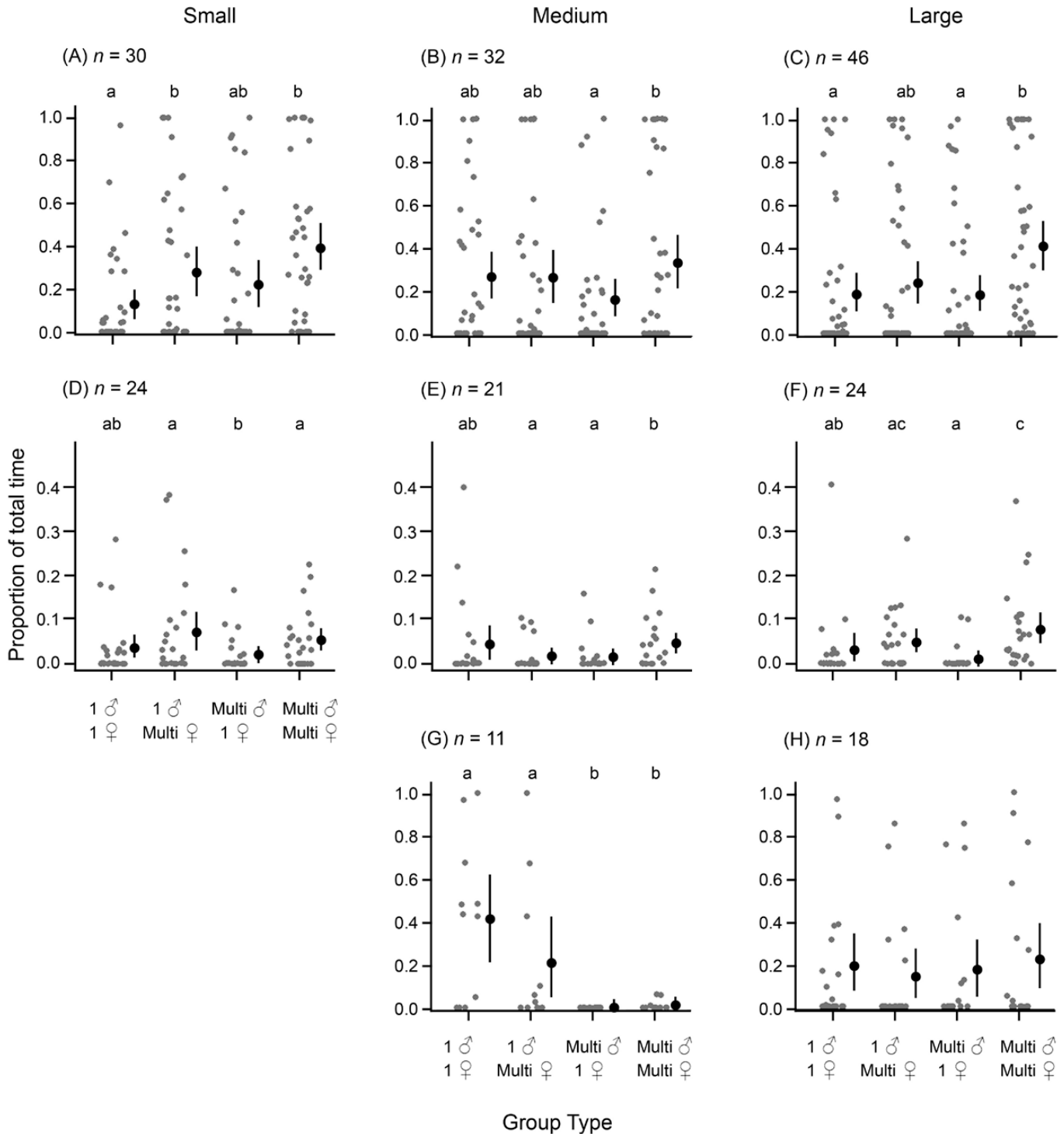
Fig. 1.—Proportion of time that small, medium, and large mule deer males and white-tailed deer males devoted to early stage courtship (A, D); late-stage courtship (B, E); and foraging (C, F). Grey dots show raw data, vertical lines at right show the 95% BCa CI, and horizontal lines the $\bar{X}$. The $\bar{X}$ [95% BCa CI] for late-stage courtship incorporates zero and non-zero values. GLMs were used in analyses, with early-stage courtship having a Poisson distribution, late-stage courtship a binomial, and foraging a Gaussian distribution (after adding a constant and logging). Different letters above size columns represent significant difference ($P \leq 0.05$) between those sizes.

$P < 0.001$; $\Delta\bar{X}$ [95% CI]: small versus medium, 0.05 [0.01, 0.11]; large versus small, 0.04 [0.01, 0.10]). In contrast to the small difference in early-stage courtship, medium and large males were >10 times more likely to engage in late-stage courtship than small males (Fig. 1B; small, 3% of males, medium 33%; large, 39%; binomial GLM: $\chi^2 = 7.343$, 2 d.f., $P = 0.025$; Odds Ratio [95% CI]: medium versus small, 14.48 [2.09, 100.46]; large versus small, 17.18 [2.60, 113.75]). Mule deer males that engaged in late-stage courtship devoted, on average, about two-thirds of their time to this activity ($\bar{X}$ [95% CI]: medium: 0.67 [0.53, 0.82], $n = 11$; large: 0.68 [0.56, 0.79], $n = 18$).

We found no differences between the time different size classes of white-tailed males devoted to early-stage courtship (Fig. 1E; Poisson GLM: $\chi^2 = 3.316$, 2 d.f., $P = 0.191$; $\Delta\bar{X}$

[95% CI]: small versus medium, −0.01 [−0.04, 0.02]; small versus large, −0.02 [−0.05, 0.02]); or their likelihood of late-stage courtship (Fig. 1F; small, 8% of males, medium 18%; large, 29%; binomial GLM: $\chi^2 = 2.454$, 2 d.f., $P = 0.293$; Odds Ratio [95% CI]: medium versus small, 3.17 [0.39, 25.51]; large versus small, 5.24 [0.72, 38.05]). Our failure to detect a size difference for late-stage courtship may be due to the relatively small number of white-tailed males of any size observed in this activity. Similar to mule deer, white-tailed males that engaged in late-stage courtship devoted about two-thirds of their time to this activity (medium and large males combined, $\bar{X}$ [95% CI] = 0.64 [0.51, 0.77], $n = 12$).

Medium and large mule deer mule deer males spent a smaller proportion of their time foraging than small males
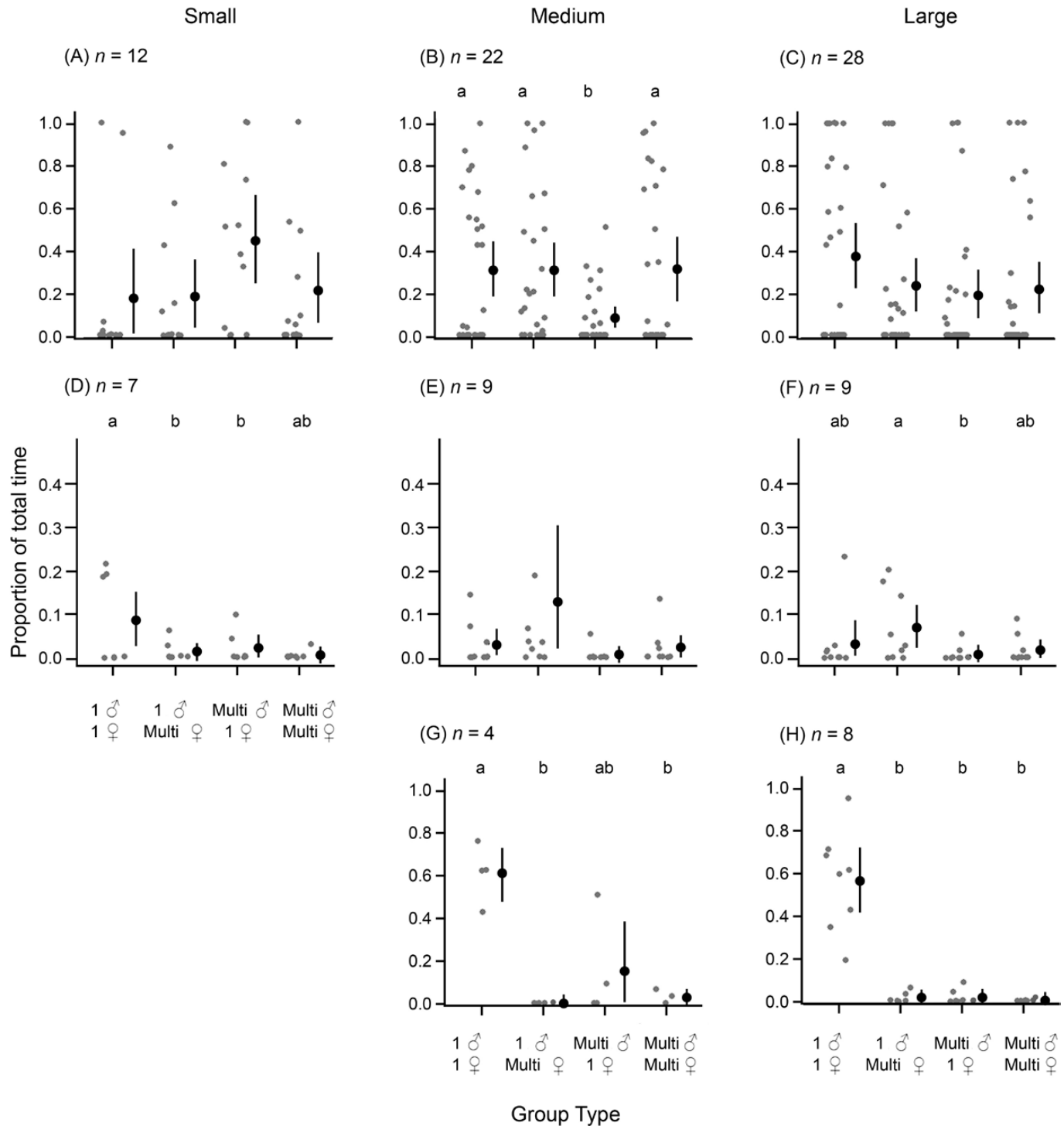
Fig. 2.—Proportion of time that small, medium, and large mule deer males spent in each male-female group type. Grey dots show raw data, vertical lines at right show the 95% BCa CI, and horizontal lines the $\bar{X}$. Top panels (A, B, C) represent overall activities (non-courtship, early-stage, and late-stage courtship combined); middle panels (D, E, F) early-stage courtship; and bottom panels (G, H) late-stage courtship. Males that did not court females were excluded from the illustration of early- and late-stage courtship. Group types: isolated pair (1♂ 1♀), single male/multiple female (1 ♂ Multi ♀), multiple male/single female (Multi ♂ 1 ♀), multiple male/ multiple female (Multi ♂ Multi ♀). GEEs with a Poisson distribution were used for analyses. Different letters above group types columns represent significant difference between those group types ($P \leq 0.05$).

(Fig. 1C; GLM: $F_{2,141} = 3.672$, $P = 0.028$; $\Delta\bar{X}$ [95% CI]: small versus medium, 0.12 [0.01, 0.22]; small versus large, 0.14 [0.05, 0.23]). We found no size difference in the time white-tailed males spent foraging (Fig. 1F; $F_{2,82} = 1.080$, $P = 0.345$; small versus large, 0.12 [−0.02; 0.26], medium versus large, 0.11 [−0.01; 0.23]).

Prediction 2, Social context of courtship.—Size did not affect the time a mule deer male spent in groups with females

Fig. 3.—Proportion of time that small, medium, and large white-tailed males spent in each male-female group type. Grey dots show raw data, vertical lines at right show the 95% BCa CI, and horizontal lines the $\bar{X}$. Top panels (A, B, C) represent overall activities (non-courtship, early-stage, and late-stage courtship combined); middle panels (D, E, F) early-stage courtship; and bottom panels (G, H) late-stage courtship. Males that did not court females were excluded from the illustration of early- and late-stage courtship. Group types: isolated pair ($1\male$ $1\female$), single male/multiple female ($1\male$ Multi $\female$), multiple male/single female (Multi $\male$ $1\female$), multiple male/ multiple female (Multi $\male$ Multi $\female$). GEEs with a Poisson distribution were used for analyses. Different letters above group types columns represent significant difference between those group types ($P \leq 0.05$).

($\bar{X}$ [95% CI]: small = 0.76 [0.63, 0.85], medium = 0.83 [0.72, 0.91], large = 0.74 [0.63; 0.84]). In contrast to mule deer, small white-tailed males spent less time than larger males in groups with females (small = 0.43 [0.26; 0.62], medium = 0.72 [0.58; 0.83], large = 0.67 [0.52; 0.79]).

When examining the four types of mixed sex groups, we found that males of all three size classes, from both species, spent more time in isolated pairs as courtship advanced, compared with the type of groups they formed during their general activities and early-stage courtship (Figs. 2 and 3). As predicted, the tendency to occupy isolated pairs as courtship advanced was more pronounced for medium than for large mule deer. Although large mule deer males spent a larger proportion of their time in multi male-multi female groups than in isolated pairs during their general activities (Fig. 2H; Poisson GEE: $\chi^2 = 6.350$, 3 *d.f.*, $P = 0.049$; isolated pairs versus multi male-multi female, $\Delta\bar{X}$ [95% CI]: −0.22 [−0.39, −0.03]), large males spent a similar proportion of their time in the four group types during late-stage courtship (Fig. 2H; $\chi^2 = 0.978$, 3 *d.f.*, $P = 0.807$; $\Delta\bar{X}$ for pairwise comparisons ranged from −0.03 to 0.08 and CI overlapped substantially).

In contrast to large males, nearly all medium mule deer males were the sole males in a group when they engaged in late-stage courtship, and most commonly they were in an isolated pair (Fig. 2G; $\chi^2 = 144.65$, 3 *d.f.*, $P < 0.001$; e.g., isolated pairs versus multi male-multi female groups, $\Delta\bar{X}$ [95% CI]: 0.40 [0.20, 0.62]). We did not find the same difference in behavior between size classes of white-tailed males. Both medium and large white-tailed males courted females almost exclusively in isolated pairs during late-stage courtship (Fig. 3G,

medium: $\chi^2 = 144.090$, 3 *d.f.*, $P < 0.001$; e.g., isolated pairs versus multi male-multi female groups, $\Delta\bar{X}$ [95% CI]: 0.58 [0.43, 0.72]; Fig. 3H, large: $\chi^2 = 94.382$, 3 *d.f.*, $P < 0.001$; isolated pairs versus multi male-multi female groups, 0.56 [0.42, 0.72]). Small males of both species were excluded from the analysis of late-stage courtship, because we observed only one small male per species engaged in late-stage courtship.

Consistent with the prediction that smaller males might adopt a group residency tactic, small mule deer males were more likely than large and medium males to stay in one group (Fig. 4; binomial GLM: $\chi^2 = 3.365$, 2 *d.f.*, $P = 0.039$; Odds Ratio [95% CI]: small versus medium, 9.16 [1.10, 68.79] small versus large, 8.46 [1.16, 61.69]). This contrasts with small white-tailed males, which were equally as likely as medium and large males to move from one group to another (Fig. 4; $\chi^2 = 0.000$, 2 *d.f.*, $P = 1.000$).

Contrary to the prediction of opportunistic concurrent courtship, small and medium mule deer males did not spend more time courting females when larger males were preoccupied by courting other females in the same group compared to times when the larger males were not courting (Mann–Whitney *U* test: small and medium: $n = 11$, $W = 5.000$, $P = 0.293$; small and large: $n = 29$, $W = 47.500$, $P = 0.778$; medium and large: $n = 18$, $W = 10.000$, $P = 0.554$). Although a second male sometimes investigated a female while a larger male tended a female in a group, we did not observe different males tending females simultaneously within the same group.

Prediction 3, Male interactions with females.—Contrary to prediction, there was little variation in the specific form of male courtship for males of both species. All large mule deer
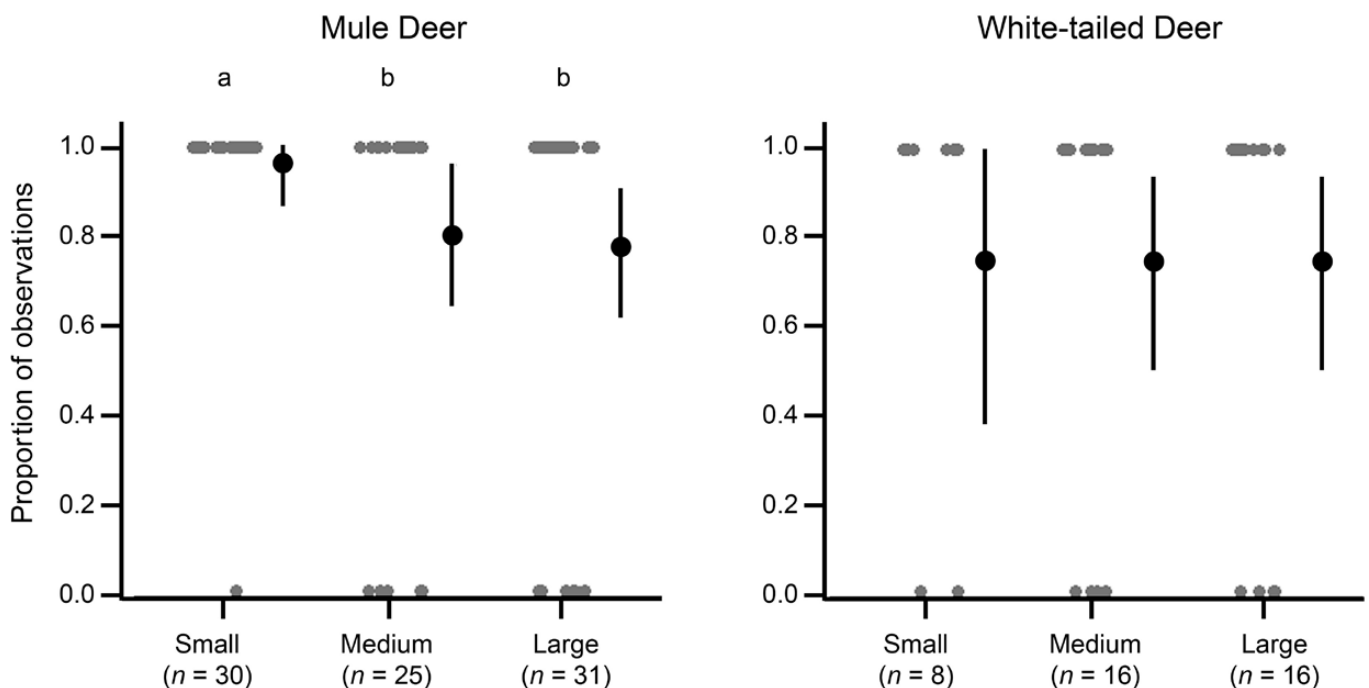
Fig. 4.—Proportion of observations males stayed in one group of females for the duration of the focal observation, based on their size and species. Grey dots show raw data, vertical lines at right show the 95% BCa CI, and horizontal lines the $\bar{X}$. Analyses were done using a binomial GLM. Different letters above size columns represent significant differences ($P \leq 0.05$) between male sizes.

males tended females during late-stage courtship, as did 80% (8 of 10) of medium mule deer males, and the sole small mule deer male that engaged in late-stage courtship. The two exceptions were medium males that used blocking to isolate females during their late-stage courtship. For white-tailed deer, males of all three size classes only used tending during late-stage courtship.

Discussion

We found that mule deer males varied their courtship effort based on their body size, as indicated by small mule deer males devoting more time to foraging and being less likely to engage in late-stage courtship than larger males. White-tailed males showed similar trends for these two behaviors; our failure to detect a significant size difference may be due to the smaller sample for this species. A striking difference between the species was that mule deer males varied the social context of courtship depending on their size, with no indication of a corresponding difference for white-tailed males. All size classes of males, from both species, increased the time they spent in one-male groups—specifically isolated pairs—as courtship advanced, suggesting an effort to reduce competition (Preston et al. 2003). However, this trend was most pronounced for medium mule deer males, and for all size classes of white-tailed deer. In contrast, large mule deer males spent a similar proportion of time tending females in all group types. Another size difference found only in mule deer was that small mule deer males appeared to adopt a residency strategy, as they were less likely than larger males to move between groups. Specific tactics used by males that differed in size were remarkably similar. Most males, from both species, tended females during late-stage courtship, with the only exceptions being two medium mule deer males that isolated females by blocking. Molecular studies are needed to determine how observed variation in courtship tactics translates to breeding success.

Although mule deer and white-tailed deer are closely related, fundamental differences in their sociality may influence the courtship tactics used by different sizes of males within each species. Mule deer are more gregarious than white-tailed deer (Lingle 2003), and larger more cohesive groups facilitate the social and aggressive tactics that mule deer employ against predators (Lingle 2001; Lingle and Pellis 2002). Their greater sociality is reflected in the larger mixed sex groups mule deer form during the reproductive season, and in increased tolerance among mule deer than white-tailed males (Airst and Lingle 2019). Here, we assess how different size classes of males adjust their reproductive tactics, within the broader context of behaviors that differ between the two species.

Our results suggest that small mule deer males devoted less energy to courtship than larger males, with much less evidence of a similar trend for small white-tailed males. Although small mule deer males devoted more of their time to early-stage courtship than other males, this increase of ~5% was relatively small. In contrast, larger mule deer males were over 10 times as likely as small males to engage in late-stage courtship, and

spent two-thirds of their time tending (or blocking) these females. The sustained nature of late-stage courtship appears energetically demanding with the male focused on one female for hours or even a few days (Hirth 1977; Kucera 1978; Geist 1981; Airst and Lingle 2019).

The failure of small males to engage in late-stage courtship may result from their inability to compete with other males, not from a lack of motivation to court females. However, small mule deer males did not move among groups as frequently as larger males, as would be expected if they actively searched for mates. One reason that small mule deer males may be less likely than large males to engage in courtship may be the need to consume food during the rut to meet their maintenance requirements (Yoccoz et al. 2002; Mysterud et al. 2004). Because small males are still growing, the food they consume prior to the rut goes to increasing their body size, which can improve their reproductive success in subsequent years (Yoccoz et al. 2002). In contrast to small males, larger males often amass sizable fat reserves before the breeding season, which enables them to forgo feeding and devote more time to courting (Yoccoz et al. 2002; Foley et al. 2018). Consistent with this logic, small mule deer males devoted more time to foraging than did larger males. These results point to a tradeoff between foraging and the time devoted to late-stage courtship (Saboraki 2019).

We found a similar, but non-significant, trend in white-tailed deer, with large males tending to spend less of their time foraging than small or medium males. However, in contrast to mule deer, white-tailed males from the three size classes were equally likely to move among groups, which we interpret as a reflection of the effort males devoted to searching for a mate. We did not find a significant difference between the probability of small versus larger white-tailed males engaging in late-stage courtship, although this analysis was hindered by a small sample. Overall, these results are consistent with the interpretation of movement and body mass data by Foley et al. (2015, 2018), which indicate that even young adult (~2-year old, which is probably comparable to our small size category) white-tailed males devote considerable effort to reproduction and mate searching. Our observations add complementary detail about events occurring at a fine behavioral scale. Although smaller white-tailed males were less likely to occupy groups with females, they spent a similar proportion of their total time investigating females. Unlike adult males, Foley et al. (2015) reported that yearling white-tailed males moved less than adult males and lost less mass. Although such findings seem likely to apply to yearling males in both the white-tailed and mule deer populations we studied, we cannot verify these results because we did not include yearling males as focal subjects.

Mule deer, but not white-tailed males, altered the social context of courtship depending on their size. Although all sizes of males showed a tendency to isolate themselves from other males as courtship progressed, this tendency was most pronounced in medium mule deer males, and in all size classes of white-tailed males. This likely was done to reduce competition and the risk of being confronted by larger males (Preston et al. 2003; Jones et al. 2011). Tending males often appear to follow

females (Kucera 1978), so the female's role in determining the movement and composition of groups during courtship needs investigation.

Large mule deer males were equally likely to tend females in groups with other males and in groups with no other males. In fact, large mule deer males tended females in groups that had only one female and multiple males as often as they tended females in the three other group types (isolated pair, one male-multiple female, multiple male-multiple female), raising the question of why multiple males sometimes remained near tending pairs. Small males using surreptitious or opportunistic tactics may explain this pattern, as has been reported for other cervids (Pemberton et al. 1992; Holand et al. 2012). On several occasions, we observed a tending male leave a female to confront another male or to investigate a different female. In six cases (four mule deer, two white-tailed deer), these separations resulted in an opportunity for a smaller male that either was within or close to the group to court the female. In the cases that we observed, the original male returned to the female and displaced the smaller male before courtship could progress. Nonetheless, it is plausible that subordinate mule deer males occupying groups alongside a tending pair might be waiting for opportunities such as these to arise.

Another difference between medium and large mule deer males was that only medium mule deer used blocking, although it was uncommon even for them, occurring in only two of 10 late-stage courtship focal observations for that size class. Blocking seems to be a coercive tactic designed to force females into isolated pairs (Hogg 1984; Clutton-Brock and Parker 1995), which was the most common group type used by medium mule deer males during late-stage courtship. Small mule deer males likely did not use blocking because they were not large enough to make it effective. Large males probably were less likely to use blocking as they may be more attractive to females and more capable of defending females from the advances of other males (McElligott et al. 2001; Charlton et al. 2007). We rarely observed blocking despite population characteristics—a high male to female sex ratio and a large proportion of large males in the mule deer population (Airst 2017; Airst and Lingle 2019)— that should have promoted stiff inter-male competition and alternative tactics such as blocking.

By remaining in a group with females, even in the presence of other males, small mule deer males may have the possibility of finding a mate through a residency strategy, in which a male gets first access to a female entering estrus before a larger male detects her (Sorin 2004) or by concurrent courtship (Airst and Lingle 2019). Previous work has shown that aggression among mule deer males does not increase significantly as courtship progresses and seldom prevents a male from joining the group (Airst and Lingle 2019). Here, we obtained no evidence that small or medium-sized males delayed their courtship until the larger male courted a different female. Courting around larger males may therefore be a strategy available to mule deer males of all sizes. This option does not appear to be readily available to white-tailed males, due to higher levels of aggression by males during late-stage courtship (Airst and Lingle 2019).

Demographic characteristics of the mule deer and white-tailed populations may have affected the reproductive opportunities for smaller males when compared with deer studied at other locations. The large size of most males (74% of mule deer, 83% of white-tailed deer were identified as medium or large) at our study site suggests that most of these individuals were at least 3 years old (see previous description of size categories in methods). If so, this age structure contrasts sharply with white-tailed populations examined in most genetic studies, which appear skewed toward the younger age groups (Sorin 2004; Foley et al. 2015; Turner et al. 2016). An older male age structure (Clutton-Brock et al. 1997; Newbolt et al. 2017) or high adult survival (Willisch et al. 2012) can limit breeding opportunities for smaller males. The predominance of larger (medium and large) males both in the mule deer and white-tailed populations may therefore have restricted breeding opportunities for small males at our location compared with other places where white-tailed deer have been studied.

Demographic characteristics also may have accentuated species differences in courtship behavior. Female-biased populations provide smaller males with increased opportunities to find females (Clutton-Brock et al. 1997; Newbolt et al. 2017). The white-tailed deer population on this site was more female-biased than the mule deer population (male: female = 1:2.6 versus 1:1.6, respectively, Airst and Lingle 2019). The white-tailed population also had a larger proportion of all female groups (Airst and Lingle 2019), likely reflecting a species difference in sociality (Lingle 2003). Even when the sex ratio is nearly 1:1 for both species, white-tailed females are more likely to form smaller all female groups and mule deer females to form larger mixed sex groups (Lingle 2003). These demographic and species characteristics would have given small white-tailed males greater opportunities to find untended females through roving and, conversely, could have promoted a residency strategy in small mule deer.

We found evidence of size-related alternative mating tactics in mule deer but not in white-tailed males. These findings give credence to the idea that there is no such thing as species-wide or population-wide breeding strategies, but rather that individuals in populations modify their courtship behavior to maximize their own success (Isvaran 2005). Molecular studies are required to determine the breeding success of these courtship strategies, and to determine whether small males of either species use surreptitious tactics that we were unable to recognize. If small mule deer do have similar levels of reproductive success as do small white-tailed males (Sorin 2004; DeYoung et al. 2009; Foley 2015; Turner et al. 2016), the differences we detected between their behavior suggest that small males from the two species would use different strategies to achieve this success.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Male size guide.

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