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Research Article

Aggressive Behavior of White-Tailed Deer at Concentrated Food Sites as Affected by Population Density

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ABSTRACT Concentrated food sources are used frequently in white-tailed deer (*Odocoileus virginianus*) management and research, but because such food sources are easily defended, aggressive interactions among deer may influence their effectiveness. The objectives of this study were to determine if deer population density or season affect 1) the order or degree of social dominance among different age and sex groups of white-tailed deer, 2) the rate at which aggressive interactions occur, 3) the severity of interactions, and 4) the extent to which subordinate groups avoid dominant groups. We conducted our study in South Texas using 2 sets of 3, 81-ha enclosures managed at varying deer population densities. We captured aggressive interactions using digital trail-cameras placed at sites with spatially concentrated food. We found that bucks $\geq$2 years of age were dominant over all other age and sex groups in $\geq$87% of their interactions regardless of deer density or season. The odds of a buck dominating over a doe increased by 10% (95% CI = 0–21%) for each additional deer/km^2 during summer, but density had little effect in any other season. Yearling bucks were dominant in 81% (95% CI = 51–100%) of their interactions with does during spring, whereas during other seasons we found no clear order to the dominance hierarchy. Social dominance between yearling bucks and does was not affected by population density. The rate of aggressive interactions increased by 2% (95% CI = 1–3%) for each additional deer/km^2 and did not differ by season. Ten percent (95% CI = 6–14%) of interactions involved more violent behaviors that we characterized as severe; this percentage did not change with population density or season. At all population densities, during all seasons, does avoided bucks at sites with concentrated food; however, the degree of avoidance declined with increasing deer density in all seasons except spring. Our results indicate that as population density increases, so do social pressures that may limit access of subordinate age and sex groups to concentrated food sites. Therefore, concentrated food sites are not equally accessible to all age and sex groups of deer and the effectiveness of such sites in deer management and research may become increasingly limited as population density increases. © 2013 The Wildlife Society.

KEY WORDS aggressive behavior, dominance, *Odocoileus virginianus*, population density, South Texas, white-tailed deer.

White-tailed deer (*Odocoileus virginianus*) are recreationally and ecologically important and therefore the target of extensive management and research efforts (Côté 2011, Hansen 2011, Jacobson et al. 2011). Because deer behavior and population parameters are influenced by nutrition, manipulation of food resources is a common management approach (Fulbright and Ortega-S 2006, Hewitt 2011). Spatially concentrated sources of nutrition may be necessary to meet some management and research objectives. Bait, for example, is used to trap deer (Schemnitz 2005), attract deer for harvest to control densities in suburban areas (Bowman 2011), and estimate deer abundance using cameras (Jacobson et al. 1997, DeYoung 2011). Concentrated food sources also are used to deliver medication such as acaracides in the northeastern United States and southern Texas to control blacklegged ticks (*Ixodes scapularis*) and cattle fever ticks (*Rhipicephalus* spp.), respectively (Pound et al. 2000, 2009;

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Rand et al. 2000). Where legal, some wildlife managers use concentrated food sources as bait and nutritional supplements to help meet harvest and population goals (Grenier et al. 1999, Jacobson et al. 2011, Murphy 2011). Furthermore, concentrated sources of nutrition occur naturally, such as some forms of mast, preferred but rare browse plants, and mineral licks.

Aggressive interactions function to build and maintain social hierarchies in many cervids including white-tailed deer (Thomas et al. 1965, Michael 1968, Hirth 1977). Social hierarchies may restrict access to concentrated food sources for subordinate age and sex groups (Appleby 1980, Grenier et al. 1999). Social dominance of mature bucks is well-documented and has been observed at mineral licks (Harmon 1978), in populations of captive white-tailed deer (Townsend and Bailey 1981), and in winter deeryards (Ozoga 1972). Aggression from dominant bucks may limit the time that more submissive does can access a concentrated food source (Grenier et al. 1999), resulting in a greater proportion of males consuming supplemental feed than females (Bartoskewitz et al. 2003). Dominance hierarchies affect feeding behavior because submissive animals may not approach a concentrated food source when dominant animals are present but instead will wait nearby and feed once dominant animals depart (Ozoga and Verme 1982).

Social interactions among deer at a concentrated resource may limit access to the resource for certain individuals or demographic groups and thus limit success in achieving management objectives and bias sampling in research activities. Pathogens and parasites may spread at sites of concentrated food (Miller et al. 2003), and different visitation patterns by age and sex groups may influence disease spread. Moreover, the rate and intensity of aggressive interactions may be positively related to deer density, such that increasing deer density may magnify the importance of dominance hierarchies in determining an individual's access to resources (Albon et al. 1992).

Previous research on intraspecific interactions of white-tailed deer primarily has been conducted on captive animals in small, highly controlled enclosures (Taillon and Côté 2007) or on free-ranging animals where little control was possible (Hirth 1977, McCullough 1979, Grovenburg et al. 2012). We sought to test how population density affects social interactions at concentrated food sources in an environment that was more natural than captive experiments and more controlled than experiments with free-ranging animals, enabling us to monitor and adjust population density. The objectives of our experiment were to determine if population density or season affect 1) the order of the social hierarchy and the degree of dominance, 2) the rate at which aggressive interactions occur, 3) the severity of interactions, and 4) the extent to which subordinate groups avoid dominant groups at sites with spatially concentrated food.

STUDY SITE

We conducted our study on the Comanche Ranch (28.28°N, 100.09°W) and the Faith Ranch (28.28°N, 100.00°W) near Carrizo Springs in Dimmit County, Texas, USA, in the Western Rio Grande Plains. Terrain in this area varied from flat to low rolling hills. The area had many ephemeral but no perennial streams. Vegetation cover was dense chaparral dominated by honey mesquite (*Prosopis glandulosa*), guajillo (*Acacia berlandieri*), blackbrush acacia (*Acacia rigidula*), twisted acacia (*Acacia schaffneri*), and cenizo (*Leucophyllum frutescens*) on the uplands with granjeno (*Celtis ehrenbergiana*), whitebrush (*Aloysia gratissima*), and guayacan (*Guaiacum angustifolium*) in lower areas. Common cacti were prickly pear (*Opuntia engelmannii*) and tasajillo (*Cylindropuntia leptocaulis*). Common grasses included red grama (*Bouteloua trifida*), curly mesquite (*Hilaria belangeri*), tobosa grass (*Pleuraphis mutica*), four-flowered trichloris (*Trichloris pluriflora*), pink pappusgrass (*Pappophorum bicolor*), and buffelgrass (*Pennisetum ciliare*; Grahmann 2009).

Western South Texas region is semi-arid with annual precipitation averaging 593 mm but highly variable (Norwine et al. 2007). Temperatures are characterized by hot summers and mild winters. Average annual temperature in South Texas was 21° C between 1900 and 2000, with an average daily low of 14.5° C and high of 28.0° C (Norwine et al. 2007).

METHODS

We established 3, 81-ha enclosures surrounded by a 2.4-m net wire fence topped with a single strand of barbed wire at each of the 2 ranches. We managed 1 enclosure at each ranch at a low (target density = 12; realized density = 11–21 deer/km^2), medium (target density = 31; realized density = 30–51 deer/km^2), and high (target density = 50; realized density = 51–98 deer/km^2) target density. Realized densities generally were greater than target densities because targets were before the reproductive pulse each year. These densities represented moderately low to high deer densities in this region of Texas (DeYoung 1985). Minor overlap in the range of realized densities between our medium (30–51 deer/km^2) and high (51–98 deer/km^2) density treatments should not have unduly affected our results because we used the actual density in each sampling period during analysis and the overlap was minimal. Each enclosure had a concentrated food source consisting of a barrel feeder and a trough feeder placed 2–3 m apart; we provided pelleted feed ad libitum at each site. We provided water in a large trough 10–25 m from the concentrated food site. We monitored population size via trail camera surveys and mark-resight techniques (see below) and adjusted populations in April and December to maintain desired densities, adjust age and sex ratios (maintained between 1:1 and 2:1 females:males), and tag new animals. We made adjustments by harvest using a firearm from a helicopter or translocated animals captured using the helicopter net-gun capture method (Webb et al. 2008). We marked animals uniquely with large colored and numbered livestock tags (Allflex USA, Inc., Dallas, TX). This research was approved by the Texas A&M University–Kingsville Institutional Animal Care and Use Committee (protocol # 2009-11-5A).

Data Collection

We recorded behaviors using RC55 rapid-fire color infrared digital trail-cameras (Reconyx, Inc., Holmen, WI). We placed 1 camera at each feed site during December 2008 (period 1; winter; Comanche Ranch: 3–10 Dec, Faith Ranch: 10–17 Dec), March 2009 (period 2; spring; Comanche: 2–16 Mar, Faith: 18 Mar–1 Apr), August 2009 (period 3; summer; Comanche: 1–15 Aug, Faith: 15–29 Aug), October 2009 (period 4; autumn; Comanche: 2–16 Oct, Faith: 22 Oct–5 Nov), December 2009 (period 5; winter; Comanche: 7–21 Dec, Faith: 21 Dec–4 Jan), and March–April 2010 (period 6; spring; Comanche: 6–20 Apr, Faith: 24 Mar–6 Apr). We had sufficient cameras to collect data on 1 ranch at a time. We reduced the time between data collection periods at each ranch by sampling each ranch in succession. On 3 occasions, the number of photos taken during the initial 14-day period was less than expected and we ran cameras for up to 5 additional days. We mounted cameras on 2 metal T-posts 3 m from the trough feeder such that 1 side of the trough feeder and both sides of the barrel feeder were visible. Because of the subtle nature of the less severe interactions, we did not record interactions observed more than 3 m beyond the feeder farthest from the camera to reduce potential visibility bias. Cameras were set to take 10 pictures each time the camera's motion sensor was triggered at a rate of 1 picture/second. Because many interactions may only last a few seconds, we did not program a delay between picture sets.

When reviewing pictures, we recorded each aggressive interaction using the postures described by Thomas et al. (1965) and Hirth (1977; Table 1). When an interaction involved multiple postures, we described each posture separately but counted the entire series of postures as 1 interaction; we used the most severe posture displayed for analysis. Because aggression is not associated with a sparring match, we did not record them as aggressive interactions. However, distinguishing between a rush and a sparring match may be difficult. Sparring matches, unlike the hostile rush, are not preceded by other aggressive postures (Michael 1968, Hirth 1977). We only classified an interaction as a rush if we observed other aggressive postures before the antler fight. For each interaction, we recorded the age and sex group (adult buck, doe, yearling buck, and fawn) of the aggressor and the opponent and the aggressive postures used. When possible, we identified unique individuals using the ear tags or unique antler characteristics. When unmarked, we defined yearling bucks as an antlered deer with ≤ 6 antler points and an inside spread ≤ 25 cm. Using a dataset of $>4{,}000$ deer age and antler records from southern Texas, these criteria are expected to correctly classify 86% of yearling males and, of all animals meeting these criteria, 96% are expected to be yearlings (D. Hewitt, Texas A&M University–Kingsville, unpublished data). Yearling bucks have a more slender doe-like build than bucks ≥ 2 years. We used body type in conjunction with antler characteristics to differentiate between yearling bucks and bucks ≥ 2 years. We did not differentiate between yearling and adult does because we did not have quantifiable criteria to define each age class.

To determine how different age and sex groups use concentrated food sites, we created a timeline showing the number of individuals in each age and sex group present at the feed site. Using timestamps on the pictures, we recorded the age and sex group and tag numbers of all deer present at the feeder every 30 minutes. We used this information to calculate the number of possible pairs, referred to hereafter as dyads, present (Michener 1980). The number of dyads is the total number of unique pair combinations that can be made

Table 1. Names and descriptions of aggressive postures used to describe white-tailed deer behavior in Dimmit County, Texas in 2008–2010; behaviors are listed in approximate order of severity.

Behavior	Used by[a]	Description[b]	Source
Non aggressive dominance	All	Instigator displays no noticeable aggressive posture yet elicits a submissive response from its opponent	Donohue 2010)
Ear drop–hard look	All	Aggressor pins ears back along neck and stares intently at opponent	Thomas et al. (1965), Hirth (1977)
Head low threat	All	Aggressor displays ear drop–hard look with head and neck held low and stretched towards opponent	Hirth (1977)
Head high threat	All	Aggressor displays ear drop–hard look with head held high and head tucked	Hirth (1977)
Sidle	All	Interacting individuals display head high threat position, broadside to each other	Thomas et al. (1965), Hirth (1977)
Strike	F, D, M	Aggressor strikes opponent with 1 or both front feet	Thomas et al. (1965), Hirth (1977)
Chase	All	Aggressor chases opponent	Hirth (1977)
Rear	F, D, M	Aggressor stands on hind legs and may attempt to strike opponent with a pedaling motion of the front feet (only aggressor stands on hind legs)	Hirth (1977)
Flail	F, D, M	Interacting individuals both stand on hind legs and strike each other with a pedaling motion of the front feet	Thomas et al. (1965), Hirth (1977)
Antler threat	AM	Aggressor displays head low threat position with head tucked and antlers pointed towards opponent	Thomas et al. (1965), Hirth (1977)
Rush	AM	Interacting individuals charge at each other from the antler threat position and a hostile antler fight ensues	Thomas et al. (1965), Hirth (1977)

[a] All, all age and sex groups; F, fawns; D, does; M, males without hardened antlers; AM, males with hardened antlers.

[b] We defined the dominant animal as the animal remaining at the site of the interaction after its conclusion.

with the deer present in the picture. The types of dyads used were buck–buck, buck–doe, buck–yearling buck, buck–fawn, doe–doe, doe–yearling buck, doe–fawn, yearling buck–yearling buck, yearling buck–fawn, and fawn–fawn. When no deer were present at the specified time, we used the nearest picture containing deer within 10 minutes. If no pictures contained deer within this range, we labeled the time interval as inactive. Because of the large number of photographs generated during each sampling period, we subsampled by reviewing the first 6,000 photographs in each enclosure per sampling period. To account for any temporal variation in behavior that may occur during a 24-hour period, we read additional photographs beyond the minimum 6,000 to read an even 24-hour period. Reading this number of photos resulted in sampling an average of 7 days/enclosure/sampling period (range = 1–19).

We calculated deer population size using camera surveys. We placed 4 remote-triggered cameras (Non Typical, Inc., Park Falls, WI) at the feed site, water source, and 2 well-used trails in each enclosure for $\geq$4 weeks during autumn and again during winter. We determined the number of bucks using unique antler characteristics (Jacobson et al. 1997). We estimated the number of does and fawns using ratios of ear-tagged to untagged deer based on a Lincoln–Peterson index (Lancia et al. 2005:120): $N = n_1(n_2 + 1)/(m + 1)$, where N = estimated number of individuals, n_1 = number of marked animals, n_2 = number of photos of marked and unmarked animals, and m = number of photos of marked animals. We calculated spring and summer estimates by adjusting the winter estimate to account for known mortalities, estimated productivity, and animals added or removed during the spring population adjustments.

Statistical Analysis

Because we had a manipulative experiment and relatively few, specific questions about the influence of population size on deer behavior, we used a generalized linear mixed model, hypothesis testing approach for all analyses (Burnham and Anderson 2002:viii) and selected the appropriate distribution and link function for each response variable (Littell et al. 2006). We considered hypothesis tests related to deer population density (deer/km^2), season (autumn, winter, spring, summer), and the interaction between population density and season, to determine if population size effects changed over time; we also included a blocking factor to control for differences between ranches. To generate the best estimates of effects, we removed the interaction term when $P > 0.1$ and re-ran the model. We accounted for repeated sampling of the same enclosures over time by treating enclosures as subjects and we examined 4 potential covariance structures: first order autoregressive, variance components, compound symmetric, and Toeplitz (Littell et al. 2006). We selected the covariance structure based on Akaike's Information Criterion corrected for small sample size (AIC$_c$). We log-transformed data when necessary to meet model assumptions of normality (see Table S1, available online at www.onlinelibrary.wiley.com for our raw data).

Social dominance.—We assessed the effects of population density on the degree of social dominance between bucks and does and between yearling bucks and does based on binomial proportions (Ramsey and Schafer 2002) modeled with a binomial distribution and logit link function (Littell et al. 2006). To determine if 1 age or sex group was dominant over the other, we computed the proportion of social interactions in which a buck was dominant over a doe and the proportion of interactions in which a yearling buck was dominant over a doe for each enclosure in each season. We defined the dominant animal as the animal remaining at the site of the interaction after its conclusion. We subtracted 0.5 from the proportion of interactions won to simplify interpretation; in other words, a value of 0 indicates no clear dominance hierarchy existed between the 2 age and sex groups. In this analysis, we considered population density as a categorical variable (low, medium, and high).

To quantify the degree of social dominance between bucks and does, we used the number of social interactions in which a buck was dominant over a doe as the numerator and the total number of social interactions that occurred between bucks and does as the denominator for each enclosure in each season. Similarly, to assess the degree of social dominance between yearling bucks and does, we used the number of interactions in which a yearling buck was dominant over a doe as the numerator and the total number of interactions between yearling bucks and does as the denominator for each enclosure in each season.

Rate of interaction.—Variation in the number of deer present at the concentrated food site and different lengths of time when multiple deer are present could affect the number of aggressive interactions observed. To adjust for this, we computed a rate of social interactions, instead of examining variation in the number of interactions. We report the rate of aggressive interactions as interactions/dyad-hour as described by Altmann and Altmann (1977). We calculated the rate of aggressive interactions as $\mathrm{I/Dyads_{avg}/Dyad_{hours}}$, where I = the number of interactions observed, $\mathrm{Dyads_{avg}}$ = the average number of dyads observed, and $\mathrm{Dyad_{hours}}$ = the number hours were $\geq$1 dyad was present at the concentrated food source. We calculated the number of hours where $\geq$1 dyad was present by dividing the number of 30-minute intervals where we observed at least 1 dyad within a 10-minute range of the 30-minute mark by 2. We calculated an interaction rate for each enclosure in each season and used a mixed model as described previously to assess the effects of population density and season on the rate of aggressive interactions.

Severity of interactions.—To compare the severity of the aggressive–submissive interactions, we categorized all postures as either severe or not severe. In general, we categorized a behavior as severe if we observed physical contact between the interacting animals in the stereotyped description of that posture. The 2 exceptions we made to this were with the chase and the antler threat. Although neither of these postures necessarily incorporates physical contact, they are often done in conjunction with other severe interactions and are therefore more appropriately placed in this category

(Thomas et al. 1965, Hirth 1977). We categorized strike, chase, rear, flail, antler threat, and rush as severe behaviors; we considered all other postures not to be severe.

We assessed the effects of population density and season on the severity of aggressive interactions by computing a binomial proportion based on the number of severe interactions (numerator) and the total number of interactions (denominator; Ramsey and Schafer 2002) and modeled them using a binomial distribution and logit link function (Littell et al. 2006).

Avoidance.—We assessed the effects of deer density and season on temporal segregation between age and sex groups by studying patterns of food source visitation for bucks and does. We selected these 2 groups because they were the only demographic groups present in every enclosure during all sampling periods. To identify the degree to which these groups avoided each other, we calculated the proportion of buck–doe dyads expected if bucks and does visited feed sites randomly and the proportion of buck–doe dyads we observed during data collection periods. We computed an avoidance metric as $\text{Dyad}_{\text{exp}} - \text{Dyad}_{\text{obs}}$, such that an avoidance metric value of 0 indicated no avoidance and a positive value indicated avoidance. $\text{Dyad}_{\text{exp}} = \text{BD}_{\text{e}}/\text{All}_{\text{e}}$, where $\text{BD}_{\text{e}} =$ number of unique buck–doe dyads possible and $\text{All}_{\text{e}} =$ number of unique buck–buck, buck–doe, and doe–doe dyads possible for the population estimate in a given enclosure and season. Similarly, $\text{Dyad}_{\text{obs}} = \text{BD}_{\text{o}}/\text{All}_{\text{o}}$ where $\text{BD}_{\text{o}} =$ number of buck–doe dyads observed and $\text{All}_{\text{o}} =$ number of buck–buck, buck–doe, and doe–doe dyads observed.

We log-transformed (ln) the avoidance metric to meet the assumption of homogeneity of variance. A value of zero indicated no avoidance, but zero was undefined after transformation. Therefore, we compared predicted ln (avoidance metric) values with 95% prediction intervals to −4.06, which is ln(0.01) and represents an avoidance metric value near zero. We calculated an avoidance metric value for each enclosure in each season and assed the effects of population density and season using a mixed model as described previously.

RESULTS

Social Dominance

In general, bucks were dominant over does regardless of population density and season; the probability of dominating in an interaction varied from 0.87 during summer to 0.98 during winter (Table 2). Bucks always were dominant over yearling bucks. Bucks, yearling bucks, and does were dominant over fawns regardless of density or season. We found a weak interaction between density and season ($F_{3,\ 20} = 2.5$, $P = 0.089$). Summer was the only season with a density effect; the odds of a buck dominating over a doe increased by 10% (95% CI = 0–21%) for each additional deer/km^2 during summer ($t_{20} = 2.13$, $P = 0.046$) such that at low population densities, the probability of a buck dominating a doe was near 0.5 and increased to near 1.0 as population density increased (Fig. 1). However, this result was strongly influenced by the interactions among deer in a single enclosure where does won 55% of their interactions with bucks. In general, the effect of population density during summer was similar to the other seasons where density had little effect ($t_{20} = 1.99$, $P > 0.1$; Fig. 1).

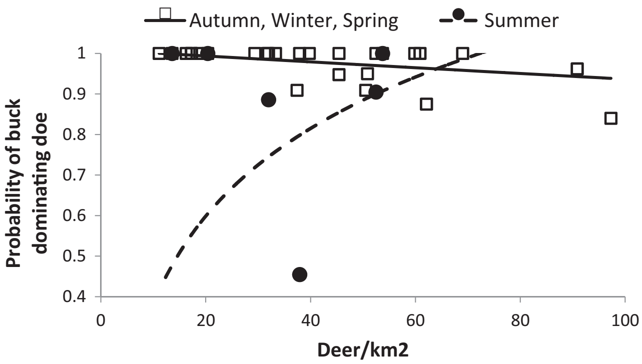

Figure 1. The probability of a white-tailed deer buck being dominant over a doe in summer (2009), autumn (2009), winter (2008, 2009), and spring (2009, 2010) averaged across 2 sites in Dimmit County, Texas. We found an overall density × season interaction, where the effect in summer differed from the other seasons.

The relationship between does and yearling bucks was far less pronounced. During summer, autumn, and winter, yearling bucks and does were equally likely be dominant in an interaction, but during spring, yearling bucks were dominant in 81% (95% CI = 51–100%) of their interactions with does ($t_{12} = 2.24$, $P = 0.045$; Table 2); the order of dominance between yearling bucks and does did not differ with population density. The degree of dominance between yearling bucks and does did not differ by season ($F_{3,\ 12} = 1.75$, $P = 0.211$), population density ($F_{1,\ 18} = 0.14$, $P = 0.710$), or their interaction ($F_{3,\ 15} = 0.74$, $P = 0.546$).

Rate and Severity of Interactions

The rate of aggressive interactions increased by 2% (95% CI = 1–3%) for each additional deer/km^2 ($F_{1,\ 25} = 10.45$, $P = 0.003$; Fig. 2). The rate of aggressive interactions did not change seasonally ($F_{3,\ 15} = 0.63$, $P = 0.606$), nor did the effect of population density vary with season

Table 2. The mean proportion (and 95% CI) of interactions in which adult buck white-tailed deer and yearling bucks were dominant when confronting a female white-tailed deer in each season from 2008 to 2010 for 2 study sites in Dimmit County, Texas.

	Summer		Autumn		Winter		Spring	
	Mean	CI	Mean	CI	Mean	CI	Mean	CI
Bucks	0.87	0.79–0.96	0.95	0.87–1.03	0.98	0.92–1.04	0.98	0.92–1.04
Yearling bucks	0.38	0.10–0.75	0.60	0.23–0.96	0.60	0.31–0.89	0.81	0.51–1.00

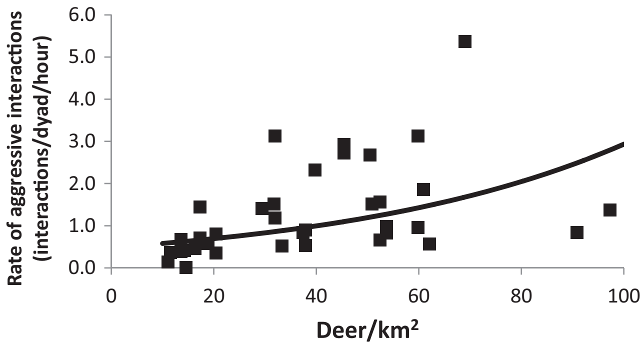

Figure 2. The effect of population density on the rate at which aggressive interactions (interactions/dyad-hr) occurred between white-tailed deer at concentrated food sites from 2008 to 2010 averaged across 2 sites in Dimmit County, Texas.

($F_{3,\ 22} = 0.54$, $P = 0.66$). Although the rate of interactions increased with deer density, severity of interactions did not ($F_{1,\ 25} = 0.05$, $P = 0.833$). The proportion of interactions that were severe was 0.103 (95% CI $= 0.064$–0.142) and was not influenced by season ($F_{3,\ 15} = 0.29$, $P = 0.834$) or a density × season interaction ($F_{3,\ 22} = 0.12$, $P = 0.948$).

Avoidance

We calculated the avoidance metric from the expected and observed proportions of buck–doe dyads which ranged 0.34–0.60 and 0.00–0.42, respectively. Because none of the 95% prediction intervals for ln(avoidance metric) contained -4.06, we concluded that all values of the avoidance metric were >0 and that does and bucks avoided one another at concentrated food sites. The lowest predicted ln(avoidance metric) occurred during summer at high population density and was -2.55 (95% prediction interval $= -3.15$ to -1.95), which corresponds to an untransformed value of 0.08 (95% prediction interval $= 0.04$–0.14). Furthermore, only 2 of the 36 untransformed avoidance metric values were smaller than 0.1 (Fig. 3), supporting the idea that bucks and does are segregated at concentrated feed sites.

The degree of avoidance between does and bucks was greatest at low deer densities, but the effect of density varied by season ($F_{3,\ 23} = 2.76$, $P = 0.065$; Fig. 4). Deer density had little effect on avoidance during spring (multiplicative change $= 0.99$; 95% CI $= 0.98$–1.00) and a large effect during summer (0.96; 95% CI $= 0.94$–0.98) where does were 4.29 times more likely to avoid bucks at low density than at high densities.

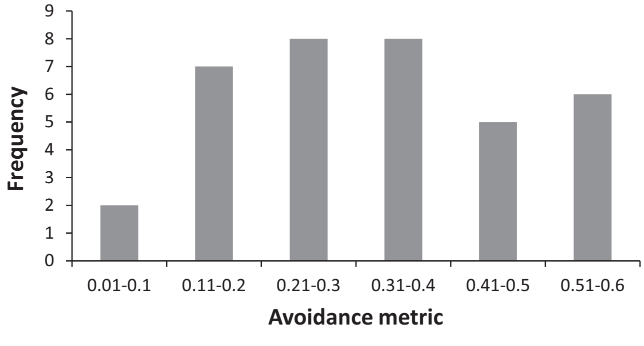

Figure 3. Frequency of avoidance metric values on 2 sites in Dimmit County, Texas. The avoidance metric indicates the degree of avoidance that occurred between white-tailed deer bucks and does; positive values indicate avoidance, negative values indicate attraction, and 0 indicates neither avoidance nor attraction.

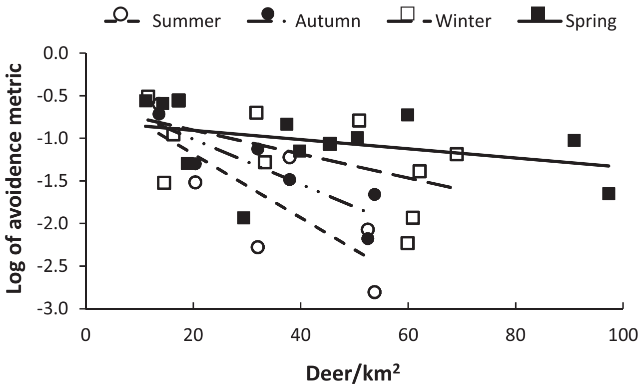

Figure 4. The effect of population density on the degree of avoidance between white-tailed deer bucks and does at supplemental feed sites during winter (2008, 2009), spring (2009, 2010), summer (2009), and autumn (2009) averaged across 2 sites in Dimmit County, Texas. Greater numbers indicate a greater degree of avoidance. The effect of density on avoidance was significant in all seasons except spring. All untransformed measures of avoidance were >0, indicating avoidance occurred throughout the study.

DISCUSSION

Dominance of bucks over all other age and sex groups of white-tailed deer is well-documented, although seasonal variation in the degree of dominance at concentrated food sites is not (Ozoga 1972, Harmon 1978, Townsend and Bailey 1981, Grenier et al. 1999). Bucks were less dominant over does during summer than other seasons. Summer corresponds to a seasonal drop in circulating concentrations of testosterone in bucks (Ditchkoff 2011). Additionally, does with fawns spend more time alert to compensate for their fawns' lack of vigilance (LaGory et al. 1981). Increased alertness during summer also may result in increased aggression (Grovenburg et al. 2009) and may be responsible for the increase in the proportion of interactions between bucks and does in which a doe was dominant. Increased doe aggression during summer may be noticeable only at low population densities when concentrated food sites have little competition for resources. As population density increased, the proportion of interactions in which a buck was dominant during the summer was more similar to the proportions observed during other seasons (Fig. 1). As population density increases, subordinate bucks may experience additional pressure from dominant bucks at the feed site and as a result, be less willing to be displaced by does.

Yearling bucks were transitioning socially from fawns to adult bucks, and thus their relationship with does changed over time. During summer, as these bucks entered the yearling age class, they won only 38% of their encounters with does. Their subordinate status may have resulted in part from does becoming aggressive towards their male offspring from the previous year, driving them out of doe groups (McCullough 1979). However, by the following spring, as these bucks approached 2 years of age, they won 81% of encounters with does and began behaving like adult bucks.

The rate of aggressive interactions increased with population density. Greater population density may have increased the proportion of time during which deer were present at concentrated food sites, leaving less time for subordinate age and sex groups to avoid dominant groups. In low-density enclosures, deer were present during 14% of time intervals sampled, whereas in high-density enclosures, deer were present in 43% of time intervals. Overlap in use of the feed site by different groups may result in the increased rate of aggressive interactions we observed. Furthermore, greater densities may result in larger groups of deer at the food site, a factor positively related to interaction rates during winter in Quebec (Grenier et al. 1999). The severity of the postures used in these interactions did not appear to be affected by either population density or season. Postures used in an interaction are highly variable and likely affected more by the social standing of the individuals involved in the interaction than by population density or season.

We found that buck–doe dyads occurred less often than expected if these 2 groups formed dyads at random, regardless of density or season. Because bucks are clearly dominant over does based on proportion of interactions in which bucks were dominant, the low proportion of buck–doe dyads at concentrated food sites indicates that does avoid these sites when bucks are present. As population density increased, the degree to which does avoided bucks decreased, which again may indicate that as population density increases, greater social pressure occurs at concentrated food sites. Increased social pressure may cause does to have difficulty avoiding the site when bucks are present and more does may attempt to feed while bucks are present rather than waiting for them to leave. Furthermore, if population density is high enough to reduce the abundance of high quality forage, does may become more dependent on food provided at such sites, spend more time at feed sites, and be more likely to encounter a buck as a result. Does that are not willing to feed when bucks are present may wait outside the feed site for extended periods of time for an opportunity to feed. This behavior pattern may extend beyond the area immediately surrounding the feed site. Bucks collared with a global positioning system unit in the high-density enclosures spent more time near the feed sites at night than similarly collared does (Garver 2011). Although this relationship only existed at night, this period is when deer forage most actively (Ozoga and Verme 1982). If social factors prevent does from spending time in the vicinity of the feed site during prime foraging time, does would be required to expend more energy and time to travel to the feed site. As a result, some does may be willing to attempt to feed when bucks are present, as indicated by the decrease in avoidance and increase in the interaction rate at high population densities. Alternatively, some does may not visit the feed site at all if the likelihood of encountering a buck and being denied access to supplement is high.

The decrease in avoidance may be responsible for the positive relationship we observed between population density and rate of aggressive interactions. The effect of density on the degree of avoidance was most pronounced during summer and became increasingly less pronounced during autumn, winter, and spring. In all seasons, as population density increased, the degree of avoidance decreased. The negative relationship between density and avoidance was strongest during summer. Does experience increased nutritional demands during summer caused by the third trimester of gestation and lactation (Hewitt 2011), which may force does to become more aggressive to meet their nutritional demands. Additionally, does may become more aggressive during summer to protect fawns during interactions with other deer (Grovenburg et al. 2009). As fawns mature, they become less dependent on their dam for protection (McCullough 1979). Similarly, as the year progressed and fawns matured, does became less assertive and began to avoid the feed site to a greater degree when bucks were present.

Social hierarchies likely play an even larger role when spatially concentrated food is not provided ad libitum as is the case when baiting. Moore (2008) found that does were under-represented in baited camera surveys at our study site, which in turn resulted in population estimates relying on buck:doe ratios that were biased low (Jacobson et al. 1997). As population density increased, placement in the social hierarchy became increasingly important as competition for resources intensified (Albon et al. 1992). Increased competition may restrict female access to high quality, but spatially concentrated, food sources and, in turn, limit the effect of supplemental feeding on productivity and survival.

MANAGEMENT IMPLICATIONS

Social interactions among deer should be considered when concentrated food sources are provided to white-tailed deer for management or research. Aggressive interactions influence patterns of deer visitation to sites of concentrated food and failure to account for the effects of social interactions could compromise management projects or bias research results. Our results suggest reducing deer density will reduce aggressive interactions at concentrated food sites and may improve access of subordinate animals.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. Raw data concerning aggressive interactions among white-tailed deer at concentrated food sites in Dimmit County, Texas from 2008 to 2010.