

INTERSPECIES INTERACTIONS BETWEEN
AXIS (*Axis axis*) AND FALLOW (*Dama dama*) DEER
AT SUPPLEMENTAL FOOD PATCHES

THESIS

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By

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ABSTRACT

In Texas and elsewhere, the introduction of exotic deer species and the creation of sympatric multispecies assemblages has increased. However, little information on interspecific behavioral interactions and contest competition exists. I observed the number of displacements between axis deer (*Axis axis*) and fallow deer (*Dama dama*) categorized by age (adult vs. yearling male), sex, and species at patches of supplemental feed. Behaviors used in displacements in order of estimated energy cost included direct approach (low cost), ritualized display (mid-cost), and bodily contact (high cost). Characteristics of the populations of both species of inter- and intraspecific herds at food patches were recorded in an attempt to correlate them with displacement patterns. Axis males performed fewer interspecific displacements than fallow males in autumn ($G = 19.3$, d.f. = 3, $p = 0.0002$) and winter ($G = 25.03$, d.f. = 3, $p < 0.0001$), while fallow males performed fewer interspecific displacements than axis males in summer ($G = 24.83$, d.f. = 3, $p < 0.0001$). Fallow females engaged in fewer displacements than axis females in the spring ($\chi^2 = 7.702$, d.f. = 1, $p = 0.0055$). The distribution of behaviors used to perform displacements did not differ between conspecifics and heterospecifics for either species. Heterospecific displacements between axis and fallow males were correlated primarily with the proportion of fallow males in hard antler at feed lines. Fallow female displacements were correlated primarily with season. I conclude that interspecific dominance interactions between these species are resolved by differences in antler morphology and aggressiveness.

INTRODUCTION

The stocking of exotic deer with functional niches similar to native species on ranches in Texas has made the study of interspecific behavior and competition an important issue for wildlife biologists. In the Edwards Plateau region of Texas, introduced exotics increase forage demands on habitats that are often overpopulated by white-tailed deer (*Odocoileus virginianus*), and may outcompete such native species by utilizing a greater variety of forage (Baccus *et al.* 1983). The introduction of exotic ungulates into Texas began in the 1920s, and populations and the number of species stocked have continued to increase (Demarais *et al.* 1998, Mungall and Sheffield 1994). Traweek (1995) estimated 195,483 individuals comprised of 71 exotic species and subspecies to be either confined (60%) or free-roaming (40%) in the state in 1994. Studies of Texas exotic and native populations have often focused on scramble competition (common utilization of finite resources: Demarais *et al.* 1998, Henke *et al.* 1988, Baccus *et al.* 1983), while studies in Europe have examined the effects of contest competition (active exclusion of other individuals from a resource) between exotic ruminants (Vankova *et al.* 1999, Bartos *et al.* 1996). Agonistic interactions regulate contest competition and are usually based on some cost/ benefit ratio associated with use of a disputed resource (Enquist and Leimar 1983, Clutton-Brock *et al.* 1979). This study focused on the behavioral interactions within and between the two most common exotic deer in Texas and examined whether one species dominated the other in contests for supplemental food.

This study defines dominance as the priority of access to a resource (Morse 1974).

Privileged use of high value resources has been the basis for studies of behavioral dominance for numerous species (Hall and Fedigan 1997, Sterck and Steenbeek 1997, Barrette and Vandal 1986, Thouless and Guinness 1986, Townsend and Bailey 1981, Appleby 1980). Dominance in contest competition has also been shown between species that compete for access to food or space (Falkenberg and Clark 1998, Anthony *et al.* 1997, Wagner and Gauthreaux 1990, Nishikawa 1987, Millikan *et al.* 1985, Fisler 1977, Brown 1971). While the concept of dominance and its measurement has been debated, agonism is generally accepted as one of its components (Drews 1993, Dewsbury 1982, Deag 1977, Rowell 1974). However, the most dominant animal may not always be the most aggressive (Drews 1993, Richards 1974), and submission and subordination, rather than aggression and dominance, have been suggested as more useful in determining rank (Rowell 1974). Nevertheless, the direction of agonistic encounters (who wins and who loses) correlates with other measures of dominance and may be used to derive a hierarchy (Richards 1974).

The level and frequency of aggression can vary with the density of interactants and the value of the disputed resource (Davies and Hartley 1996, Enquist and Leimar 1987, McPeck and Crowley 1987). In situations of communal niche packing, the potential for interspecific competition increases and resources become more valuable. In these situations, a dominance hierarchy can be of greater ecological importance. A thorough knowledge of the dynamic interactions leading to dominance in high density, multi-species assemblages is important to wildlife managers because of the role of dominance in regulating aggression, which may affect the frequency of antler breakage, antler wounding, or food intake (Vankova *et al.* 1999, Mungall and Sheffield 1994, Geist

1986). Specifically, I examined interactions between axis deer and fallow deer to determine if a consistent dominance relationship exists between the two species.

Axis and fallow deer have similar body weights and herd sizes, are gregarious, and readily form multiple species groups in open woodland (Putman 1988). This similarity of herd behavior and weight facilitated studying the role of interspecific aggression in assessing multi-species dominance hierarchies by partially reducing the complications of unequal body size or herd size. Ables (1977) reported that fallow and axis deer dominated supplemental feeding areas at the Powderhorn Ranch in Calhoun County, Texas and, therefore, can be considered important participants in multi-species feeding interactions.

Fallow deer are a temperate zone adapted species (30°-80° north latitude) and stand about 90 cm at the shoulder. Buck and doe weights range at 79-102 kg and 36-41 kg respectively (Mungall and Sheffield 1994). In Texas, this species is found in 104 counties, with 56.5% of occurrences on the Edwards Plateau (Traweek 1995). Their preferred habitat on the Edwards Plateau is woodland (Goetze 1998). The rut occurs in autumn, and fawns are born in early summer (Chapman and Chapman 1975, Mungall and Sheffield 1994). The distribution of this species is so widespread in Texas, it often occurs sympatrically with other cervids.

Axis deer or chital are a tropical deer (0°-30° north latitude) and also stand about 90 cm at the shoulder. Buck and doe weights range at 66-113 kg and 43-66 kg respectively (Mungall and Sheffield 1994). In central Texas, the chital is found in 100 counties, with 80.3% of occurrences on the Edwards Plateau (Traweek 1995). Grasslands and open woodlands are preferred habitat for this deer on the Edwards Plateau

(Nowak 1991). The breeding season intensifies during the rut from mid-May to August, peaking in June and July. Fawns are born in all seasons (Mungall and Sheffield 1994).

I investigated whether or not a consistent interspecific dominance relationship between these two species existed by testing two predictions: (1) members of the dominant species should displace subordinate species members more frequently from patches of supplemental food, a high value, easily defendable resource, and (2) members of the dominant species should expend less energy in displacements than members of the subordinate species. In other words, dominant individuals do not fight for the right of access to a food patch. In addition, I censused both axis and fallow deer populations for 16 months to correlate energetically important periods, such as the rut or parturition peaks, with fluctuations in agonism or dominance behaviors.

STUDY AREA

The study was conducted at the Double D Ranch, a privately owned exotic game ranch, located near Rosanky, Bastrop County, Texas. The ranch covers 2,025 ha surrounded by a 3-m high fence. The variety of native and exotic game stocked include fallow, axis, and sika deer (*Cervus nippon*), blackbuck antelope (*Antelope cervicapra*), nilgai antelope (*Boselaphus tragocamelus*), elk (*Cervus canadensis*), American bison (*Bison bison*), aoudad sheep (*Ammotragus lervia*), eland (*Taurotragus oryx*), red lechwe (*Hydrotragus leche*), and scimitar-horned oryx (*Oryx dammah*). Three larger lakes and three or more smaller ponds provide water for animals.

During the study, approximately 114 fallow deer and 165 axis deer occupied the ranch (Gary Rose, pers. comm.). The ranch provided 4530 kgs (1132.5 kgs. per week) of Hi - Protein Buck & Doe feed (Ful-O-Pep Feeds) as supplemental food each month. Feed was dispersed on Mondays, Wednesdays and Fridays. Food plots of oats (*Avena sativa*), ryegrass (*Lolium perenne*), and/or wheat (*Triticum aestivum*) planted via a “no till” method provided an additional food source in winter.

The ranch has both woodland and open grassland habitats. Woody vegetation includes blackjack oak (*Quercus marilandica*), eastern red cedar (*Juniperus virginiana*), cedar elm (*Ulmus crassifolia*), loblolly pine (*Pinus taeda*), shortleaf pine (*Pinus echinata*), black hickory (*Carya texana*), hackberry (*Celtis laevigata*), greenbriar (*Smilax bona-nox*), yaupon (*Ilex vomitoria*) and elbowbush (*Forestiera pubescens*). Several of these species produce mast. Herbaceous vegetation includes purpletop (*Tridens flavus*),

sand lovegrass (*Eragrostis trichodes*), broomsedge bluestem (*Andropogon virginicus*), little bluestem (*Schizachyrium scoparium*), and Bermudagrass (*Cynodon dactylon*).

Bastrop County has a moderate climate with mild winters and hot summers. Winter daytime temperatures average 18° C and drop between 4° C and 9° C at night. Summer daytime temperatures average 32° C and may reach 38° C. Mean annual precipitation is 91 cm (Shrout *et al.* 1987).

MATERIALS AND METHODS

Displacement Frequency

From September 1999 through August 2000, inter- and intraspecific behavioral interactions of axis and fallow deer were observed at high quality food patches in eight pastures. Each observation period lasted 20 min with two to four observation periods/pasture/week. Immediately before observation periods, a truck dispensed supplemental food in 25 patches, each 1.5 m long and at intervals of 3.8 m. Animals feeding at the patches were observed from an elevated blind (3.6 m high) or a mobile blind (1999 Ford Ranger). An observation period began when males and females of both species arrived at food patches. Individuals of all ungulate species on the ranch were allowed to feed at patches, but only interactions involving axis and fallow deer were recorded. The initial number of males and females of both species, the number of male yearlings, the stage of antler development (velvet or hard antler), and the number of other species present at feed patches were recorded for each period by video camera (Sony TRV-9 Camcorder). If males or females of either study species were absent from patches longer than 10 min, the observation event was terminated and excluded from the analysis. Patches were scanned by eye or spotting scope (Swift full length tripod Model 792R), and all observed displacements between axis and fallow deer were tabulated. Displacements occurred at a rate that allowed events to be recorded. I recorded the species and sex of both displacer and receiver (a dyad) and the behavior used to effect displacement. For males, age and stage of antler development were

determined. In both species, yearling males typically possess single spike antlers, and this feature was used to differentiate them from adults. The data collected provided rates of occurrence, temporal change, and an unbiased sample of dyadic interactions (Altmann 1974). Because of the tendency of individuals to follow a displaced member of their sex-species cohort, even when displacement behaviors were not directed toward them, multiple individuals displaced by a single interaction were recorded as one displacement.

Displacement Behavior

Specific behaviors used to perform displacements were recorded. These behaviors can be ranked into three categories based on the aggressiveness of the action: (1) approach/ direct attention, (2) ritualized displays, and (3) contact or chase. A description of the behaviors (Table 1) associated with these three categories follow those proposed by Ables (1977) and Koutnik (1981). These behavior categories were assumed to have increased energy cost with increased aggression. To test the hypothesis that one species (the dominant one) would be less likely to have to escalate aggression to perform a displacement, I compared the distribution of displacements in these three categories between heterospecifics. In addition, I compared heterospecific displacement behaviors with conspecific behaviors to determine if either species exhibited a difference in displacement intensity between conspecifics and heterospecifics.

Supplemental Food Patch Recruitment

Each month, from March to August 2000, the number of individuals of all species at food patches was recorded every two min for 60 min to estimate recruitment to food patches. Recruitment numbers for each species were then multiplied

Table 1. Description of behaviors used to perform displacements by *Axis axis* and *Dama dama*. Behaviors are ranked into three categories based on estimated energy expenditure: low-cost approach/ direct attention, mid-cost ritualized displays, and high-cost contact displacements.

Behavior Category	Behavior	Description
Approach/ Direct attention	Approach	Actor walks or runs toward reactor resulting in the reactor leaving the patch
	Direct attention	Actor turns head toward reactor resulting in the reactor leaving
Ritualized displays	Antler threat	Actor lowers head so as to orient antlers toward reactor and may raise head rapidly, as though performing a thrust without making contact with the reactor
	Parallel walk	Actor extends and arches neck while slowly walking parallel to reactor, moving legs in a stiff manner. Snout may be raised, with eyes often rolled toward reactor. Ables (1977) reported this behavior as a head-down display.
	Head nod	Actor raises and lowers chin toward reactor without orienting antlers toward the reactor.
	Head high	Actor presents profile to reactor and raises its chin, often orienting the facing eye towards reactor
Contact	Antler contact	Actor lowers head so as to orient antlers toward reactor and moves head rapidly, making swift contact with the body of the reactor
	Flail	Actor rises on hind legs and repeatedly kicks at reactor with forelegs in a pedaling motion.
	Bite	Actor extends head toward body of the reactor and bites the reactor
	Spar	Actor and reactor join antlers and push against one another
	Kick	Actor rapidly extends foreleg to make forceful contact with the body of reactor.
	Nose	Actor contacts body of reactor with nose
	Press	Actor straddles neck or shoulders of reactor while both are facing the same direction
	Neck wrestle	Actor extends neck across neck of reactor and presses downward against the it
	Head butt	Actor forcefully extends head to make contact with the head of the reactor (Ables 1977)
	Chase	Actor pursues reactor after displacing it from a food patch

by a daily demand value in order to standardize the feeding pressure put on food patches by all species. Daily demand was calculated by multiplying an estimated live animal weight by a forage intake factor based on a percentage of live weight (Mungall and Sheffield 1994, Nowak 1983).

Census Lines

To establish the onset and duration of the rut and birthing period of both species, and consequently, increases in supplemental food value, a 17.5 km mobile route was established along roads of the ranch (Fig. 1). This mobile route was used to census fallow and axis populations two to four times per week from May 1999 to August 2000. Censuses occurred in early morning or late afternoon. During herd censuses, I recorded information on herd size, sex composition, antler development, and number of fawns under two-months of age (recorded from January to August 2000) for both species. Herds were classified as bachelor, female, or mixed herds. Females and at least one adult male composed mixed herds. Herds composed of females and male yearlings were classified as female herds. A separation distance > 50 m was used to distinguish separate herds (Braza *et al.* 1986, Clutton-Brock *et al.* 1982).

To better define rutting periods for both species, fallow harems and axis buck bellows and thrashes were recorded. A harem consisted of one hard-antlered adult male with ≥ 1 females. The number of harems observed each month was converted to a percentage of all herds seen. The frequency of axis bellows and thrashes represented the number seen or heard from axis bucks attending the feed patches during an observation period. Although this information was not recorded on a per individual basis, their occurrence was time-specific enough to pinpoint rutting activity.



Figure 1. Aerial map of the Double D Ranch at Rosanky, Bastrop County, Texas. The white line represents the mobile route used to census *Axis axis* and *Dama dama* populations.

Fawning periods were based on the frequency of occurrence on census lines of fawns ≤ 2 month old. Individual fawns may have been recounted in subsequent censuses. This measurement proved adequate for determining fawning periods but did not provide an accurate count of fawns for either species. A major bias of this method concerned the accuracy of estimating fawn age from a distance (Ables 1977).

To estimate the amount of association between axis and fallow deer on the ranch and at food patches, I recorded the presence of either species within 10 m of each other on mobile censuses from September 1999 to August 2000, and the presence of both species feeding at the same food patch at the beginning of observation sessions from May 1999 to April 2000. Simple Ratio Association Indices were calculated for herds using the formula of Karczmarski (1996):

$$AI = \frac{J}{(a + b) - j}$$

where

AI = association index for axis and fallow deer herds

j = number of sightings in which axis and fallow deer are within 10 m of each other

a = number of sightings of axis deer

b = number of sightings of fallow deer

An association index value of 0 meant that the two outermost individuals of the herds observed on censuses never occurred within 10 m of each other, or individuals of both species never occurred at the same food patch at the beginning of observation sessions. An index of 1 indicated herds observed on censuses always occurred within 10 m of each other, or individuals of both species always occurred at the same food patch at

the beginning of observation sessions. Census data from October 1999, January, March, and June 2000 were used to determine an average sex ratio for each species.

Statistical analysis

Species group size could not be controlled during observation periods, therefore, to standardize displacement frequencies between dyads, the number of displacements for a given sex-species pair was modified by dividing by the ratio of winners to losers. These converted displacement scores increased when winners were outnumbered by losers, and decreased when winners outnumbered losers. Displacement scores between all male-yearling and male-female dyads were compared by Mann-Whitney U tests.

Displacement scores between male-species dyads and female-species dyads were compared by a multisample median test. This test compared the distribution of displacement scores between conspecific and heterospecific dyads of each sex around a grand median for those dyads. These distributions were then tested for equality using maximum likelihood analysis (Zar 1999). Distributions, in effect, represented the variability around the grand median. Conspecific dyads were tested in comparison to heterospecific dyads to determine differences between interspecific and intraspecific aggression. Those species-sex groups whose displacement scores skewed above the grand median to a greater extent than other groups were considered dominant. Dyad members were grouped based on sex and species. Dyads involving yearlings were ignored in this analysis because the low overall number of interactions prohibited a reliable statistical assessment of interspecies dominance. Based on the strength of the male/female dominance pattern, the sexes were compared separately for conspecific and heterospecific interactions throughout the year. Seasonal medians were calculated using

all displacement scores within a given season. Seasons were defined as fall: September-December, winter: December-February, spring: March-May, and summer: June-August. Due to differences in the number of observation sessions per season, annual medians were calculated from each month's median score, and because of the low number of observation sessions in March and April, these two months were combined. Antler development dyads and male adult-yearling dyads for the year were also compared with a multisample median test. Displacement scores from both species were pooled into the respective categories and the proportion above and below the grand median were analyzed. Proportions were used instead of raw numbers to standardize differences in the number of displacement scores between dyads. Homogeneity in the number of sex-species groups attending food patches, percent of males in hard antler, and sex ratio were tested by ANOVA. The post-hoc Tukey-HSD was used to determine where differences lay.

Spearman Rank Correlations were used to assess relationships between displacement scores and characteristics taken from both the census route and from feed patches. These characteristics included the percent of males in hard antler, sex ratio, the number of males and females attending feed patch lines, monthly fawn occurrence, and season. Season was coded as fall = 1, winter = 2, spring = 3, and summer = 4.

I pooled male displacement behaviors into the three main categories (approach/direct attention, ritualized display, contact) based on the estimated amount of effort required performing the behavior. For female deer, ritualized displays were not obvious or easily identifiable; therefore, their displacement behaviors were classified as either contact or non-contact for both year and season. Heterospecific displacement

behavior was compared to an expected cumulative frequency distribution based on the proportion of conspecific displacement behaviors by a Kolmogorov-Smirnov test for the year-long study. I used chi-square contingency tables to test for seasonal differences or if interactions were low between species. In addition, heterospecific displacement behavior between species was compared to determine if one species escalated displacement intensity more than the other when displacing heterospecifics using chi-square contingency tables. Statistical tests were performed using SAS Version 6, SPSS for Windows, Release 6.1.4, and Statview 5.0 Power PC Version.

RESULTS

Food Patch Attendance Patterns

I conducted 88 observation sessions from September 1999 to August 2000, and recorded 2102 displacement scores, including 1412 scores of 0, where no interaction took place between a given dyad in a session. Six-hundred and sixty displacement scores (403 zero scores) were recorded for male dyads, 558 (247 zero scores) for male-female dyads, 546 (540 zero scores) for female-male dyads, and 338 (222 zero scores) for female-female dyads. The number of axis males and females at food patch lines throughout the year averaged 5.68 and 8.35, respectively. Similarly, the number of fallow males and females at patches throughout the year averaged 4.47 and 8.83, respectively. The abundance of axis and fallow deer present at food patches differed by sex ($F = 15.53$, $d.f. = 351$, $p < 0.0001$) but did not differ between species (Tukey-HSD test, $p > 0.05$). Abundance varied little throughout the defined seasons. The number of axis males attending patches differed significantly only in spring ($F = 5.3783$, $d.f. = 87$, $p = 0.002$), while fallow females attended patches in greater numbers in fall ($F = 4.0554$, $d.f. = 87$, $p = 0.0096$; Table 2). The number of yearling males attending food patches did not differ annually between species; however, axis yearlings attended food patches in greater number in fall and winter than spring and summer ($F = 11.2367$, $d.f. = 87$, $p = 0.00001$). Fallow yearling males attended food patches in greater number in spring ($F = 7.7771$, $d.f. = 87$, $p = 0.0001$; Table 2). Average sex ratios for the year differed between species ($z = -2.2799$, $p = 0.0226$). Adult sex ratios for each species differed with season. The

sex ratio for fallow deer at patches became male biased in summer ($F = 3.4563$, d.f. = 87, $p = 0.02$). Sex ratios for axis deer had a male bias in both spring and summer, but differed most in the spring when more than twice as many males attended patches as females ($F = 5.3022$, d.f. = 87, $p = 0.0021$; Table 2). The percentage of males in hard antler at food patches differed by season but not annually. Axis males had significantly larger percentages of attending males in hard antler in fall and summer ($F = 46.4146$, d.f. = 84, $p < 0.00001$), while fallow males had significantly larger percentages of attending males in hard antler in fall and winter ($F = 50.8201$, d.f. = 84, $p < 0.00001$; Table 2).

Axis and fallow deer did not tend to associate with each other at food patches. Association indices for these two species were typically zero, but ranged from 0.0 to 0.33 (Fig. 2). Even a positive association index of 0.33 indicated minimal contact between the species. Recruitment of species to patches and the demand for food in those patches were measured six times from March to August 2000 (Fig. 3 and 4). The values for association indices and demand for food as measures of potential competition showed similar patterns. Most animals arrived at a food patches within 4 min of depositing the last patch of food. Demand peaked within 6 min after depositing the last food patch. While other species were able to attend food patches during observation periods, Spearman rank correlations indicated no association between dyad displacement scores and the number of species or demand on the line.

Sex-Age Class Dominance

Adult males of both species dominated females of both species ($z = 2.971$,

Table 2. Seasonal mean frequencies (± 1 s.d.) of *Axis axis* and *Dama dama* adult and yearling males, females, sex ratios (male/female) and percent hard antlered adult males at food patches from September 1999 through August 2000 at the Double D Ranch, Bastrop County, Texas. Between season differences were tested by ANOVA and *p*-values are reported.

Species	Fall	n	Winter	n	Spring	n	Summer	n	d.f.	<i>p</i>
Adult axis males	3.67 (2.62)	27	5.25 (3.03)	24	9.2 (8.3)	15	6.23 (3.39)	22	87	0.002
Axis females	8.67 (4.76)	27	9.29 (7.47)	24	10.27 (8.12)	15	5.64 (3.4)	22	87	0.0916
Yearling axis males	1.52 (1.40)	27	2.08 (1.50)	24	0.80 (0.86)	15	0.19 (0.40)	22	87	<0.00001
axis sex ratio	0.58 (0.55)	27	0.79 (0.57)	24	2.26 (2.91)	15	1.53 (1.43)	22	87	0.0021
Percent hard antler	91.8 (21)	25	36.74 (28.7)	23	18.53 (23.59)	15	86.1 (20.49)	22	84	<0.00001
Fallow males	3.37 (1.82)	27	4.79 (2.59)	24	5.2 (4.23)	15	4.95 (4.03)	22	87	0.1895
Fallow females	10.96 (6.55)	27	8.54 (4.36)	24	9.8 (5.98)	15	5.86 (3.38)	22	87	0.0096
yearling fallow males	0.81 (0.88)	27	1.54 (1.28)	24	2.13 (1.25)	15	0.71 (0.64)	22	87	0.0001
fallow sex ratio	0.39 (0.24)	27	0.8 (0.8)	24	0.89 (1.12)	15	1.26 (1.41)	22	87	0.02
Percent hard antler	100 (0)	27	100 (0)	24	36.63 (46.1)	13	21.43 (40.53)	21	84	<0.00001

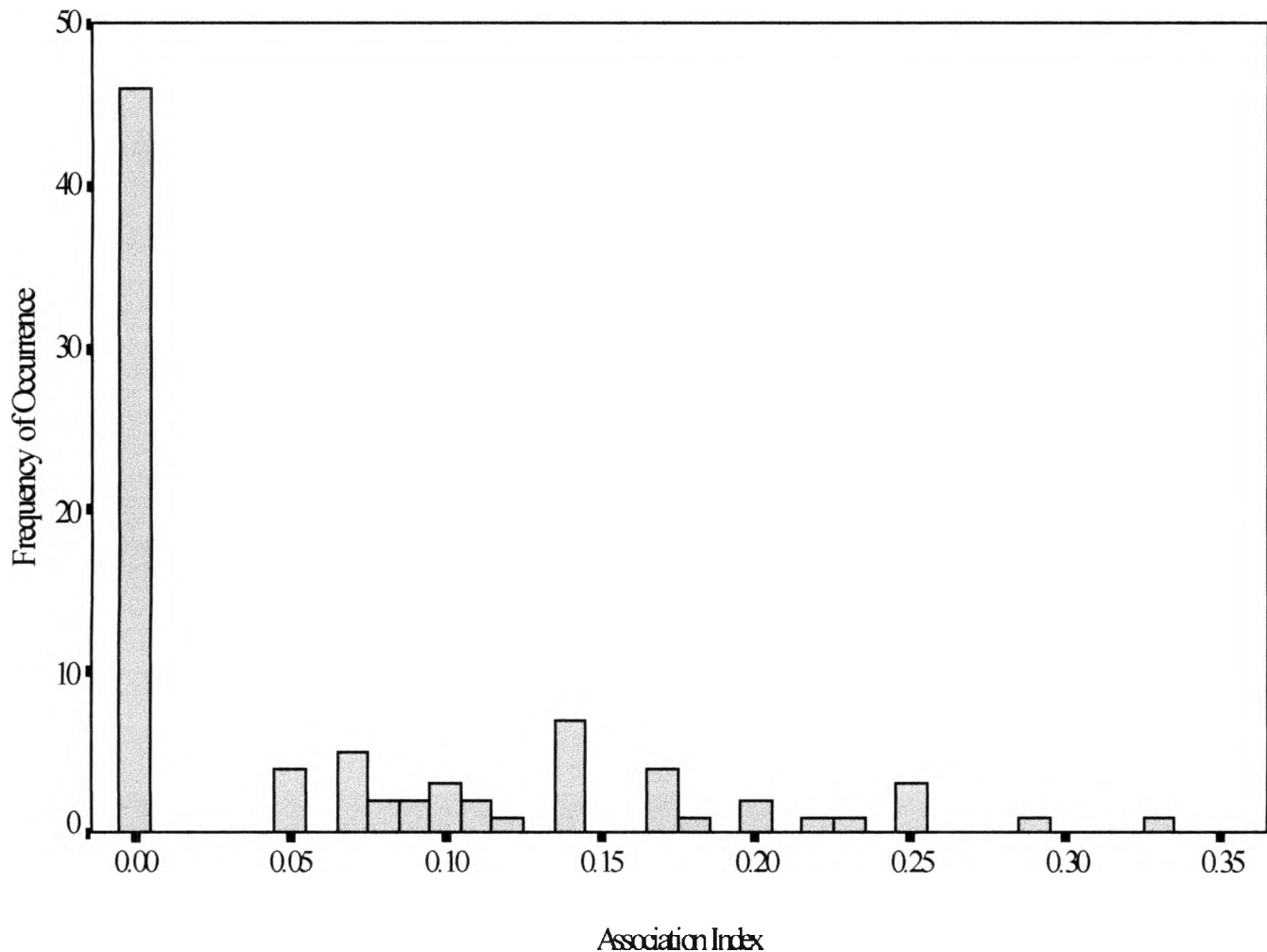


Figure 2. Association indices between *Axis axis* and *Dama dama* at supplemental food patches immediately prior to observation sessions from May 1999 to April 2000 at the Double D Ranch, Bastrop County, Texas. Species attending the same patch of food were considered in association. Association indices between these species were typically zero, with the highest index score of 0.33 occurring only once.

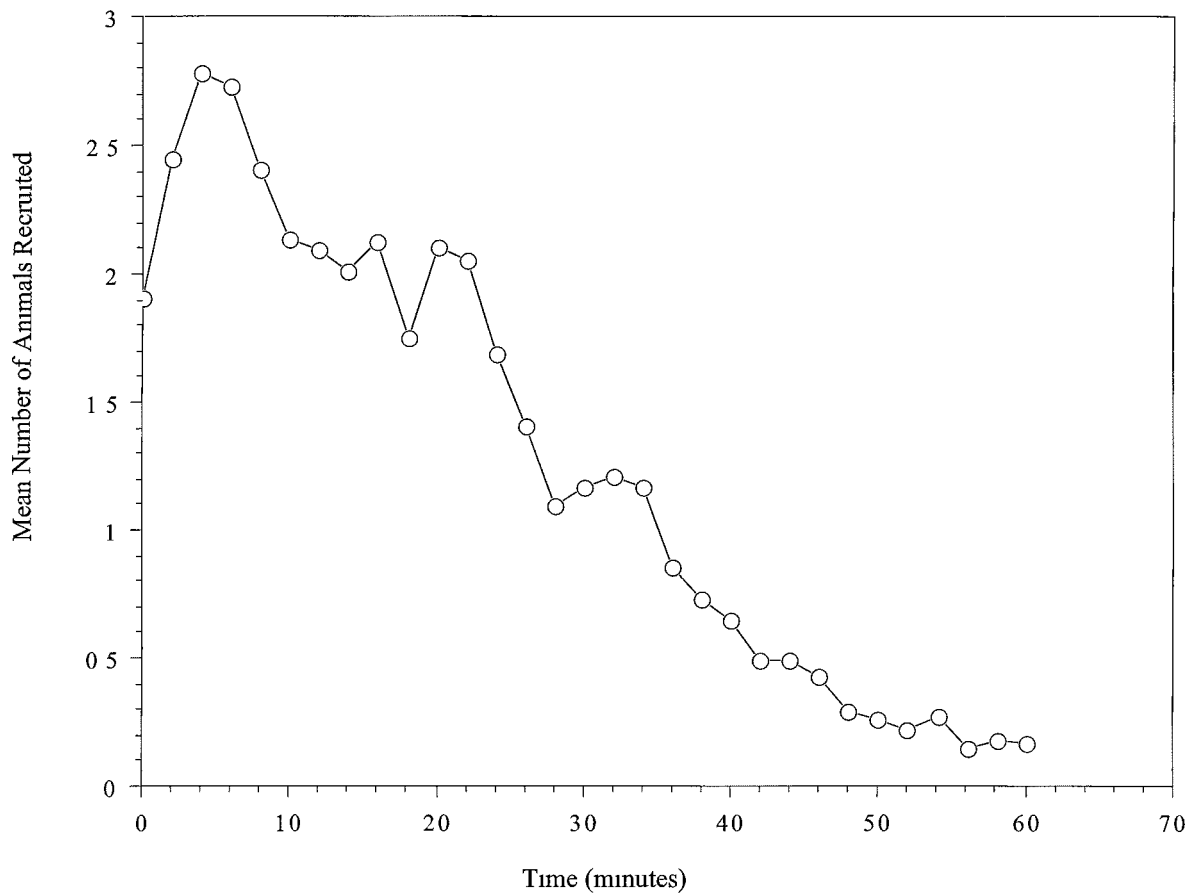


Figure 3. Average recruitment of all species at supplemental food patches based on one observation session per month from March 2000 to August 2000 ($n = 6$) at the Double D Ranch, Bastrop County, Texas. The greatest number of individuals attended patches within the first 10 min after feed deposition.

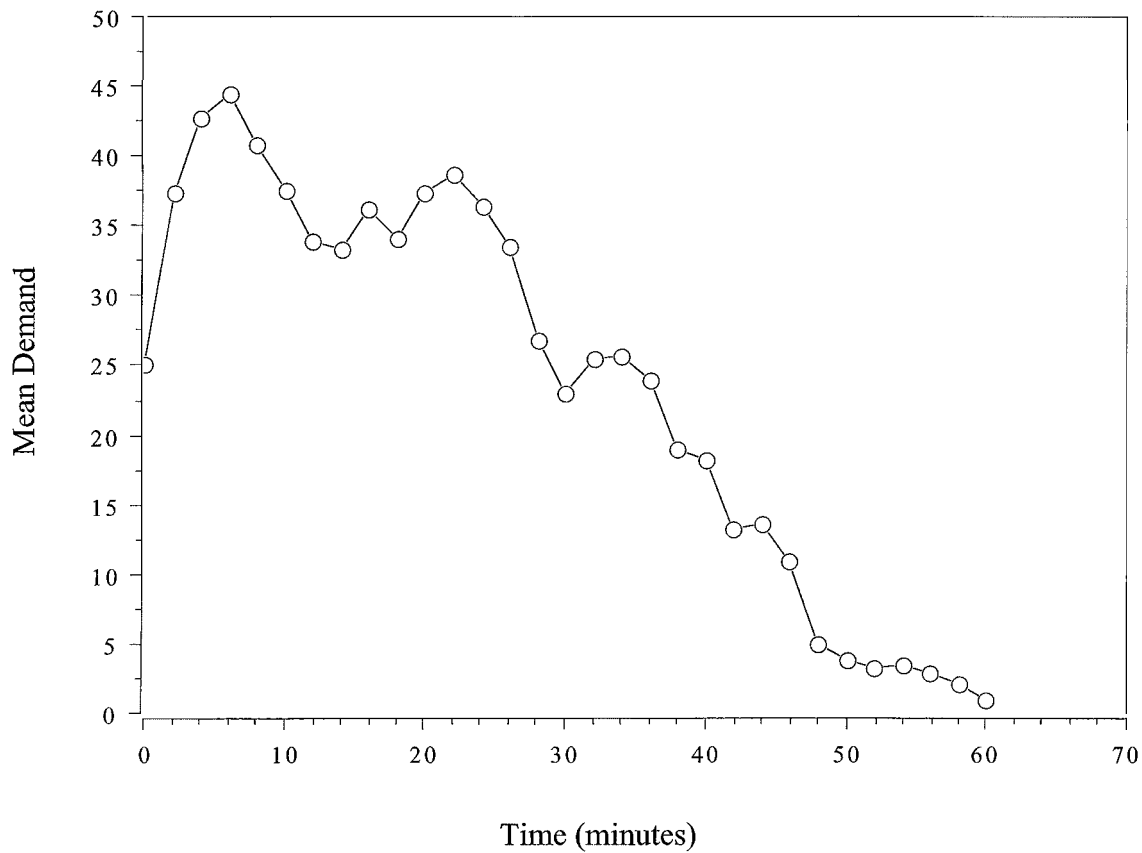


Figure 4. Average demand at food patches based on one observation session per month from March 2000 to August 2000 ($n = 6$) at the Double D Ranch, Bastrop County, Texas. Demand was calculated by multiplying the average number of ungulate species present at 25 patches of supplemental food by an intake factor based on a percentage of species body weight class. Greatest demand for supplemental feed was within the first 10 min of an observation period.

$p < 0.005$). In addition, adult males of both species dominated yearling males of both species ($z = -4.373$, $p < 0.0001$) with some exceptions depending on antler development. Finally, yearling males of both species dominated females of both species ($z = -9.748$, $p < 0.0001$).

Antler Development Dominance

Male deer dominance depended on development of antlers and stage in the antler cycle. Males of both species in hard antler had an advantage over males of both species in velvet ($G = 83.82$, d.f. = 3, $p < 0.0001$; Fig. 5). Deer of both species in velvet initiated proportionally fewer displacements toward hard-antlered deer than hard-antlered deer initiated toward deer in velvet. The advantage conferred to hard-antlered deer allowed dominance by yearlings with hard antlers of both species over adult males of both species in velvet ($G = 40.67$, d.f. = 3, $p < 0.0001$). This complicated the apparent dominance relationship between adult and yearling males, indicating that age may be less of a factor in determining dominance than an individual's antler development.

Interspecific Dominance Interactions

Males of both species demonstrated a very clear pattern of dominance during the study. Over the course of the entire study, both species displaced each other with equal frequency ($G = 2.14$, d.f. = 3, $p = 0.5434$). However, the variation in dyad displacement scores increased seasonally. In fall, axis males displaced fallow males less frequently than all other male dyads ($G = 19.3$, d.f. = 3, $p = 0.0002$), while fallow males displaced males of both species equally ($G = 0.75$, d.f. = 2, $p = 0.6860$; Fig. 6). This pattern continued through winter. During winter, axis males never displaced fallow deer from

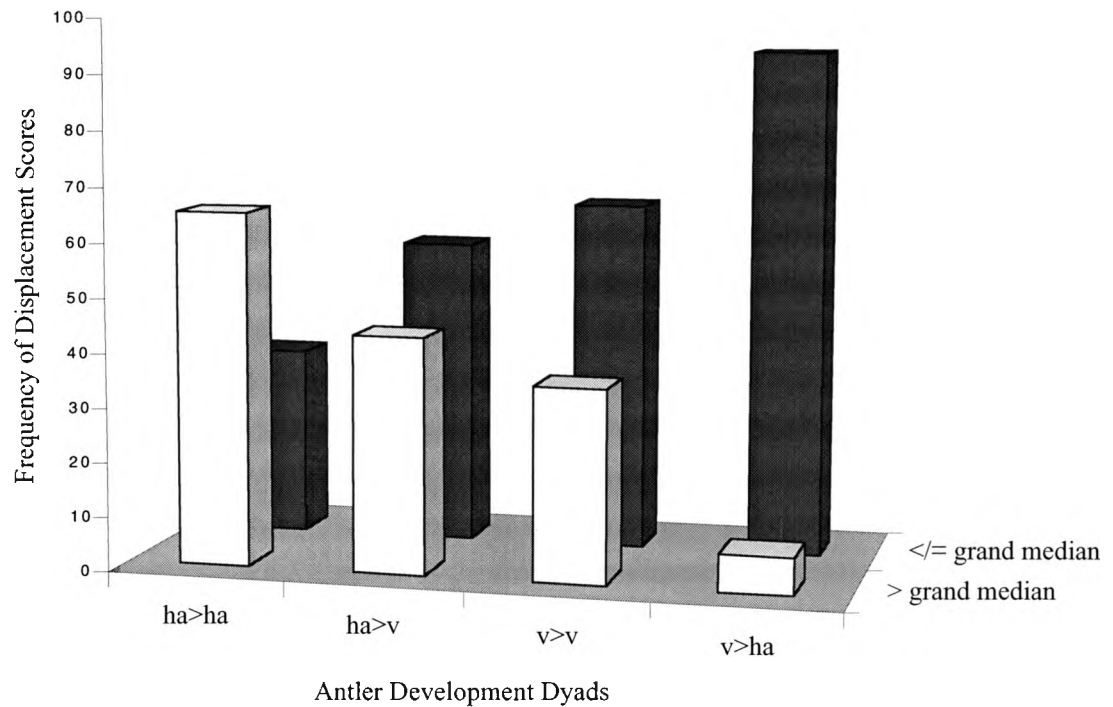


Figure 5. The variation of displacement scores around a grand median displacement score (0) for dyads of adult male *Axis axis* and *Dama dama* in hard antler (ha) and in velvet (v) from September 1999 through August 2000 at the Double D Ranch, Bastrop County, Texas. Displacement scores above (white bars) and below or equal to (black bars) a grand median displacement score for all dyads are compared with a G test. Deer in velvet displaced deer in hard antler fewer times than all other dyads ($p < 0.0001$).

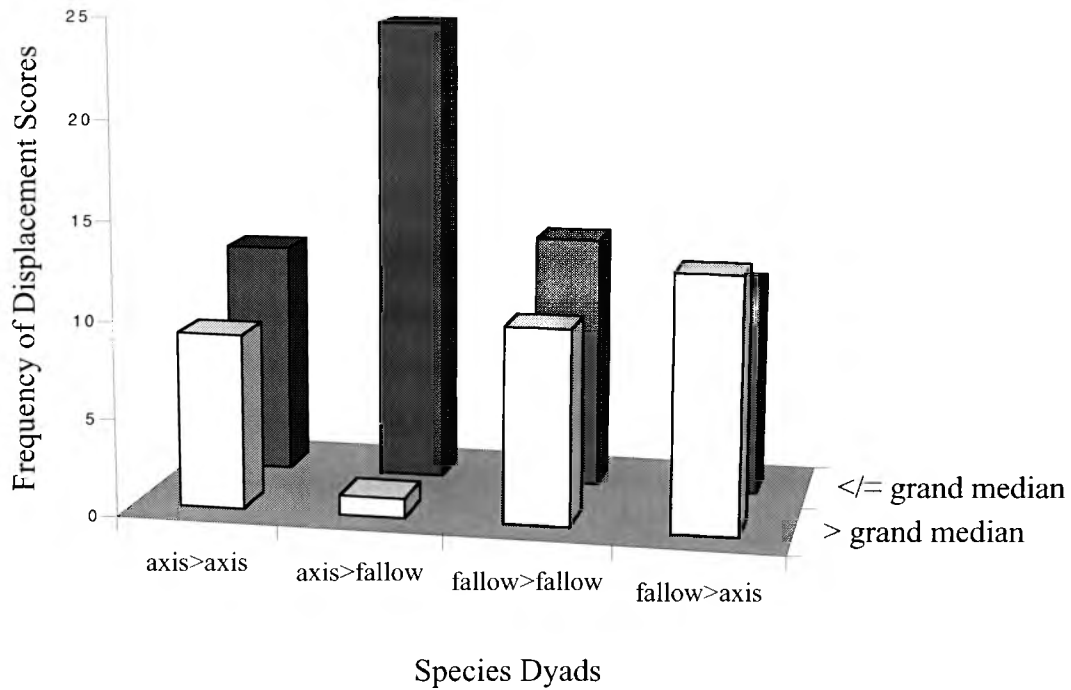


Figure 6. The variation of displacement scores around a grand median displacement score (0) for adult male dyads of *Axis axis* and *Dama dama* from September 1999 to December 1999 at the Double D Ranch, Bastrop County, Texas. Displacement scores above (white bar) and below or equal (black bar) to the grand median displacement score for all dyads were compared with a G test. The distribution of displacement scores for fallow buck conspecific and heterospecific interactions and axis buck conspecific interactions are equal but axis males displaced fallow males fewer times than all other dyads during this period ($p < 0.0001$).

food patches while all other dyad combinations had equal displacement frequencies ($G = 0.09$, d.f. = 2, $p = 0.9555$; Fig. 7). During spring, no significant difference existed between male dyad combinations of both species ($G = 1.43$, d.f. = 3, $p = 0.6997$). Dyad displacement frequencies decreased during this season with the exception of axis conspecific displacements. In summer, the pattern of fall and winter reversed (Fig. 8). Fallow bucks never displaced axis bucks while displacements by all other dyads remained equal ($G = 1.12$, d.f. = 2, $p = 0.5716$). Throughout the study, males did not escalate contests behavioral intensity when displaced by males of the other species. Increases in axis interspecific displacements did not correlate with increases in fallow interspecific displacements ($r_s = -0.0865$, $p = 0.440$). Inter- and intraspecific displacements did not correlate within species for either fallow bucks ($r_s = 0.1841$, $p = 0.122$) or axis bucks ($r_s = -0.0403$, $p = 0.735$), so high conspecific displacement scores did not necessarily indicate high heterospecific displacement scores.

Females showed less aggression than males during the study. Displacement scores of zero were significantly more common than scores > zero ($\chi^2 = 8.40$, d.f. = 1, $p = 0.0038$), making heterospecific dominance patterns less clear. Like males, no annual difference existed in the frequency of displacement scores for hetero- or conspecific dyads ($G = 1.86$, d.f. = 3, $p = 0.6019$). Fallow females had a cyclic pattern of aggression with females being most aggressive in fall and least aggressive in summer toward both conspecifics (Kruskal-Wallis $H = 9.5406$, d.f. = 3, $p = 0.0229$) and heterospecifics (Kruskal-Wallis $H = 9.4597$, d.f. = 3, $p = 0.0238$). Axis females did not demonstrate this seasonal aggression pattern between conspecifics (Kruskal-Wallis $H = 6.5357$, d.f. = 3,

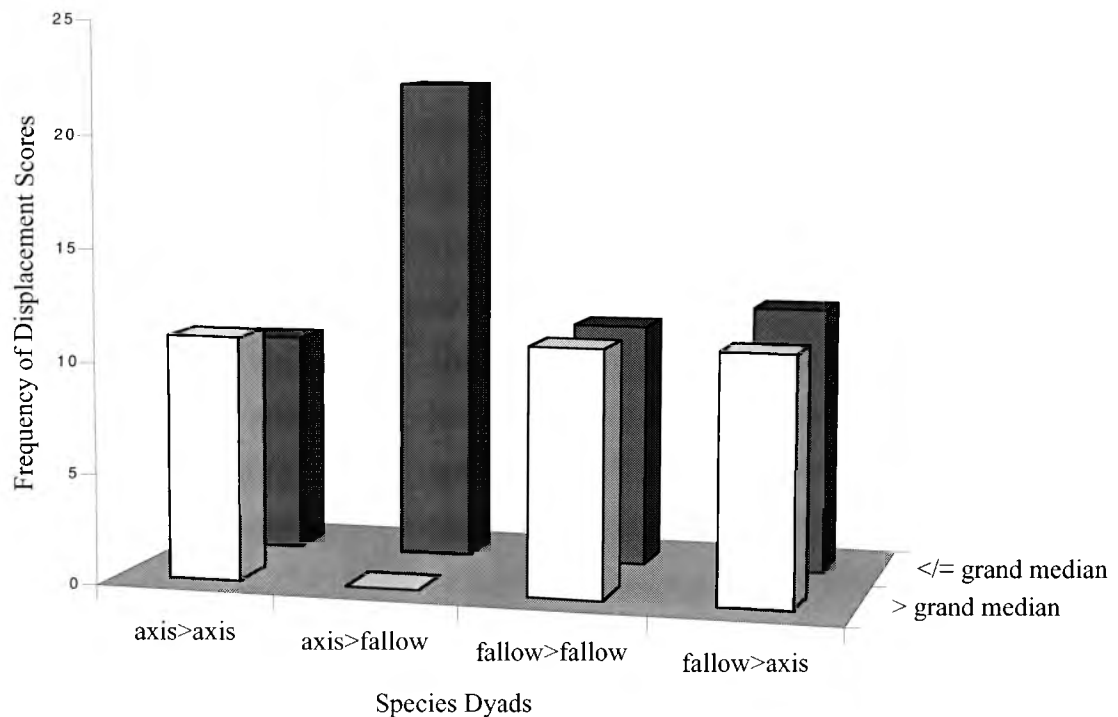


Figure 7. The variation of displacement scores around a grand median displacement score (1.45) for adult male dyads of *Axis axis* and *Dama dama* from December 1999 through February 2000 at the Double D Ranch, Bastrop County, Texas. Displacement scores above (white bars) and below or equal to (black bars) a grand median displacement score for all dyads are compared with a G test. The distribution of displacement scores for fallow buck conspecific and heterospecific interactions and axis buck conspecific interactions are equal, but axis males displaced fallow males fewer times than all other dyads during this period ($p < 0.0001$).

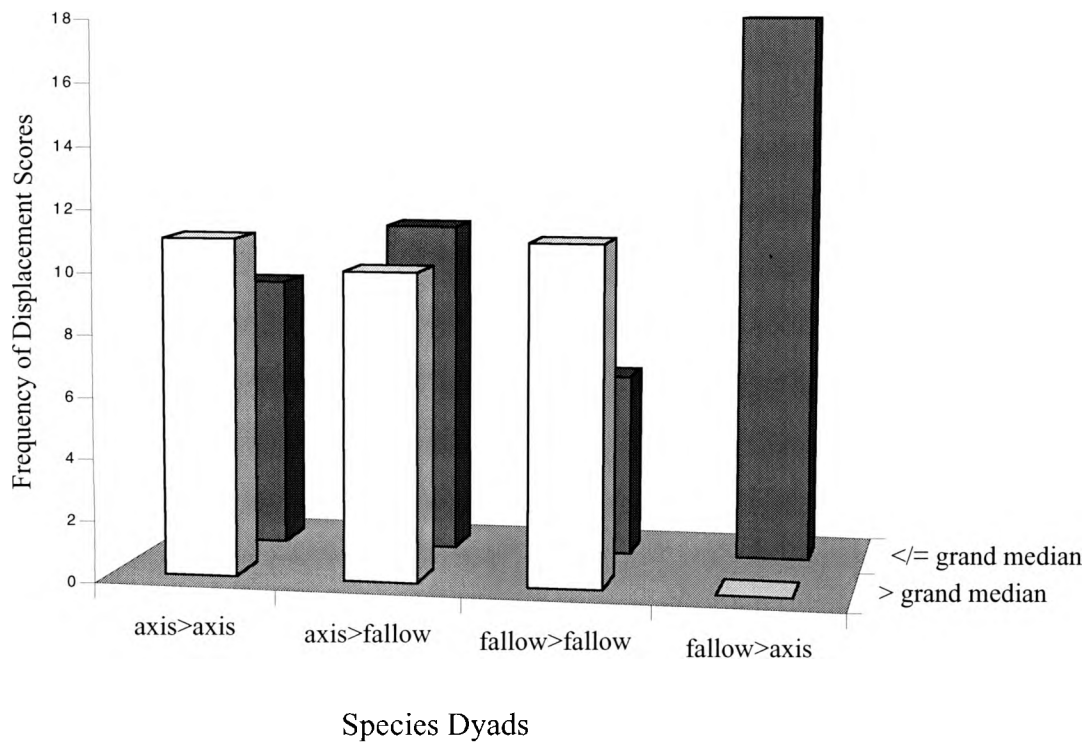


Figure 8. The variation of displacement scores around a grand median displacement score (0.875) for adult male dyads of *Axis axis* and *Dama dama* from 5 June through 28 August at the Double D Ranch, Bastrop County, Texas. Displacement scores above (white bars) and below or equal to (black bars) a grand median displacement score for all dyads are compared with a G test. The distribution of displacement scores for axis buck conspecific and heterospecific interactions and fallow buck conspecific interactions are equal, but fallow males displaced axis males fewer times than all other dyads during this period ($p < 0.0001$).

$p = 0.0883$) or toward heterospecifics (Kruskal-Wallis $H = 2.543$, d.f. = 3, $p = 0.4676$). No differences existed for displacements by either species in inter- and intraspecific dyads in fall ($G = 0.64$, d.f. = 3, $p = 0.8869$) and winter ($G = 2.57$, d.f. = 3, $p = 0.4636$). While displacement scores did not differ in fall, fallow does were less likely to initiate displacements than axis does in winter ($\chi^2 = 4.19$, d.f. = 1, $p = 0.0407$; Fig. 9). This pattern was similar to the spring pattern. During spring, axis does initiated inter- and intraspecific displacements more frequently than fallow does ($\chi^2 = 7.702$, d.f. = 1, $p = 0.0055$; Fig. 10). The distribution of inter- and intraspecific displacements were equal in both axis does ($\chi^2 = 2.521$, d.f. = 1, $p = 0.1123$), and fallow does ($\chi^2 = 0.96$, d.f. = 1, $p = 0.3272$). Displacement scores > 0 were infrequent in summer ($\chi^2 = 24.24$, d.f. = 1, $p < 0.0001$), however displacement frequencies between dyads were equal ($G = 3.91$, d.f. = 3, $p = 0.2711$).

As with males, female deer did not escalate behavioral intensity when displaced by females of the other species throughout the study. Increases in interspecific displacements between the two species did not correlate ($r_s = 0.1439$, $p = 0.181$); however, there was a positive relationship between conspecific and heterospecific displacements in axis does ($r_s = 0.3417$, $p = 0.002$) and fallow does ($r_s = 0.2867$, $p = 0.007$).

Displacement Intensity

In general, neither species had to escalate behavioral intensity more frequently to displace heterospecifics than the other annually or seasonally. In an exception to this, axis females did escalate contact level behaviors to displace heterospecific does more

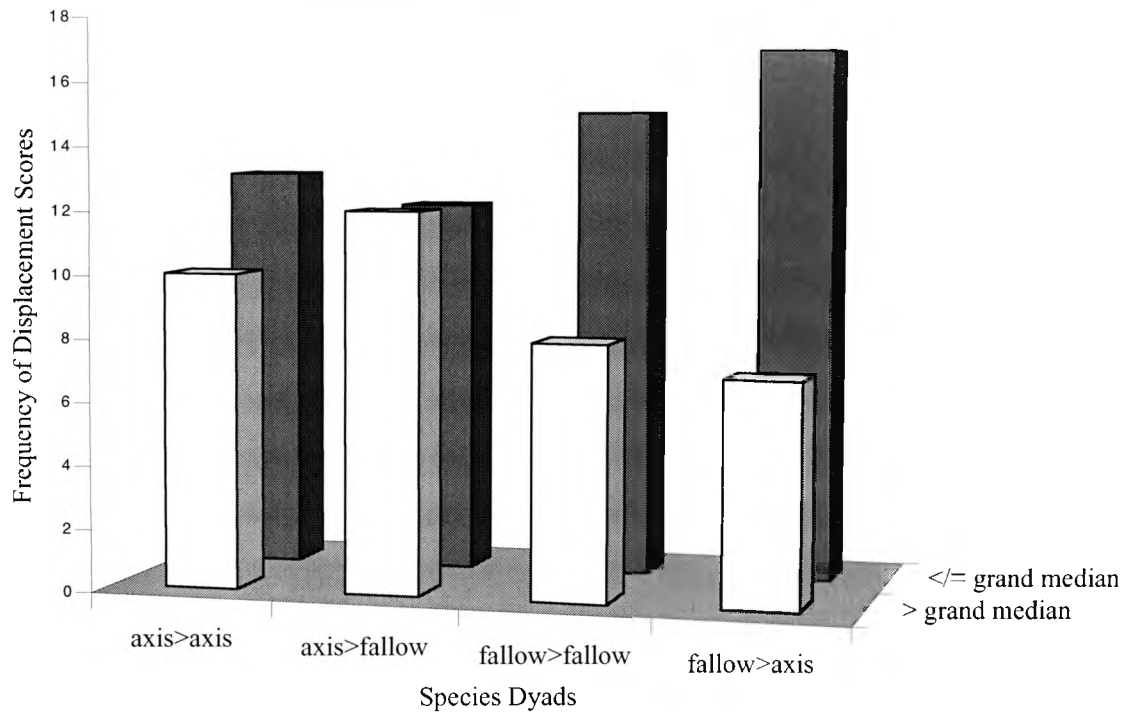


Figure 9. The variation of displacement scores around a grand median displacement score (0) for female dyads of *Axis axis* and *Dama dama* from December 1999 through February 2000 at the Double D Ranch, Bastrop County, Texas. Displacement scores above (white bars) and below or equal to (black bars) a grand median displacement score for all dyads are compared with a χ^2 test. Axis doe conspecific and heterospecific interactions were more common than fallow doe interactions during this period ($p = 0.0407$).

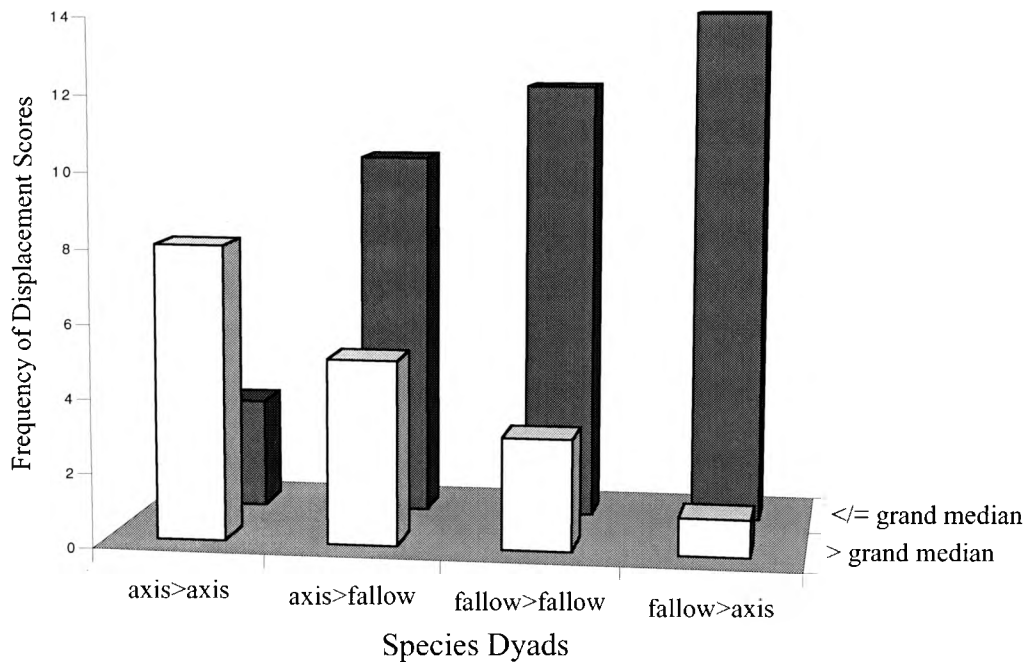


Figure 10. The variation of displacement scores around a grand median displacement score (0) for female dyads of *Axis axis* and *Dama dama* from March 2000 through May 2000 at the Double D Ranch, Bastrop County, Texas. Displacement scores above (white bars) and below or equal to (black bars) a grand median displacement score for all dyads are compared with a χ^2 test. Axis doe conspecific and heterospecific interactions were more common than fallow doe interactions ($p = 0.0055$).

often than fallow females escalated behavior to displace axis does in the fall. In winter, fallow females escalated contact level behaviors more often than axis females to displace heterospecific does (Table 3).

Similar heterospecific and conspecific displacement behaviors occurred between males of both species. Male axis deer escalated agonistic behavior against fallow males ($n = 51$) in equal frequency as expected from the 80 instances of agonism toward other axis males; however, the highest measured level of aggressive behavior (contact) tended to occur less often against fallow males than for conspecifics ($\chi^2 = 6.61$, $\alpha = 0.016$, d.f. = 1, $0.025 > p > 0.01$: Fig. 11).

Male fallow deer escalated agonistic behavior against axis males ($n = 108$) in equal frequency as expected from the 111 instances of agonism toward other fallow males. Less heterospecific contact level aggression occurred than conspecific contact level aggression ($\chi^2 = 8.10$, $\alpha = 0.016$, d.f. = 1, $0.005 > p > 0.001$: Fig. 12). Adult males of both species displaced heterospecific and conspecific yearling males and females with about equal levels of aggression (Tables 4 and 5).

Seasonal displacement behaviors were grouped into contact and non-contact displacements. In fall, axis male displacements did not differ between heterospecific and conspecific males, females, or yearling males with the exception of spring, where contact displacements were more likely to involve conspecifics (Table 6). Conversely, fallow males showed less aggression toward axis males than conspecifics in fall and winter, but displaced females and yearlings of both species with equal intensity (Table 7).

Few displacements occurred between yearling males. Axis yearling males initiated five displacements toward other conspecific yearling males but only one towards

Table 3. Seasonal comparison of heterospecific displacement intensity between *A. axis* and *D. dama* deer in seven observed dyads. Chi-square contingency analysis between non-contact displacements (N-C) and contact (C) displacements between indicates that neither species was required to escalate to contact displacement behaviors more than the other in most cases. An exception to this was that axis females were required to escalate when displacing fallow females in fall; and fallow females were required to escalate when displacing axis females in winter.

Interaction	Species	Fall		Winter		Spring		Summer	
		N-C	C	N-C	C	N-C	C	N-C	C
male vs. male	axis	1	0	4	0	14	0	29	1
	fallow	31	0	64	2	8	0	11	0
male vs. yearling	axis	7	0	4	1	2	0	8	0
	fallow	11	1	14	0	0	0	0	0
male vs. female	axis	72	2	39	4	14	0	31	4
	fallow	34	1	55	2	11	0	8	0
yearling vs. yearling	axis	1	0	0	0	0	0	0	0
	fallow	1	0	9	0	0	0	0	0
yearling vs. female	axis	16	2	19	0	0	0	0	0
	fallow	10	0	17	3	0	0	0	0
yearling vs. male	axis	0	0	0	0	2	0	1	0
	fallow	1	1	13	2	9	1	0	0
female vs. female	axis	7	9	17	1	3	3	4	2
	fallow	12	3*	4	3*	0	1	3	0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

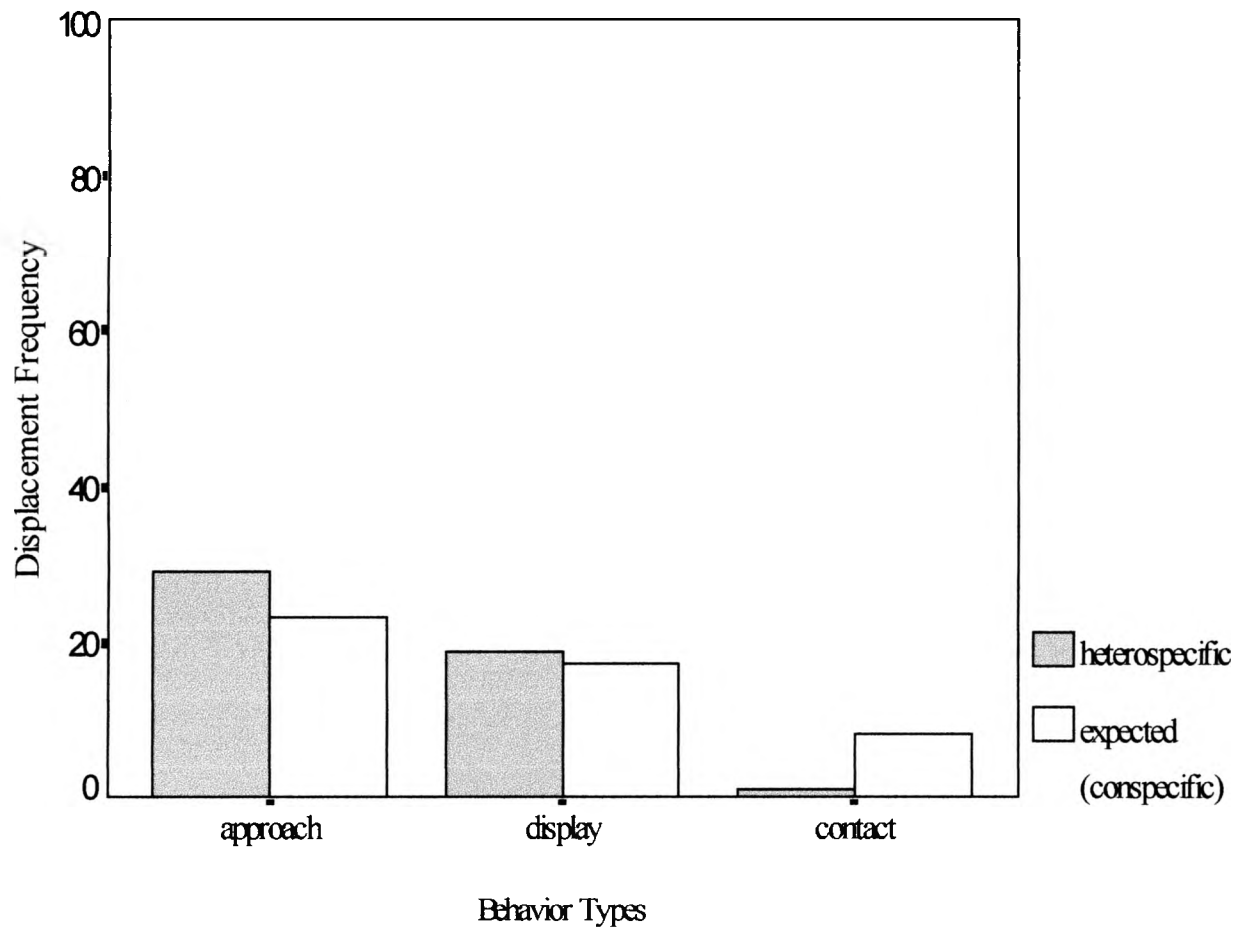


Figure 11. Distribution of heterospecific displacement behaviors compared to an expected distribution based on conspecific displacement behaviors in *Axis axis* males. The overall distribution of behaviors was not different between heterospecifics and conspecifics for approaches, displays, or contact displacements ($p < 0.10$).

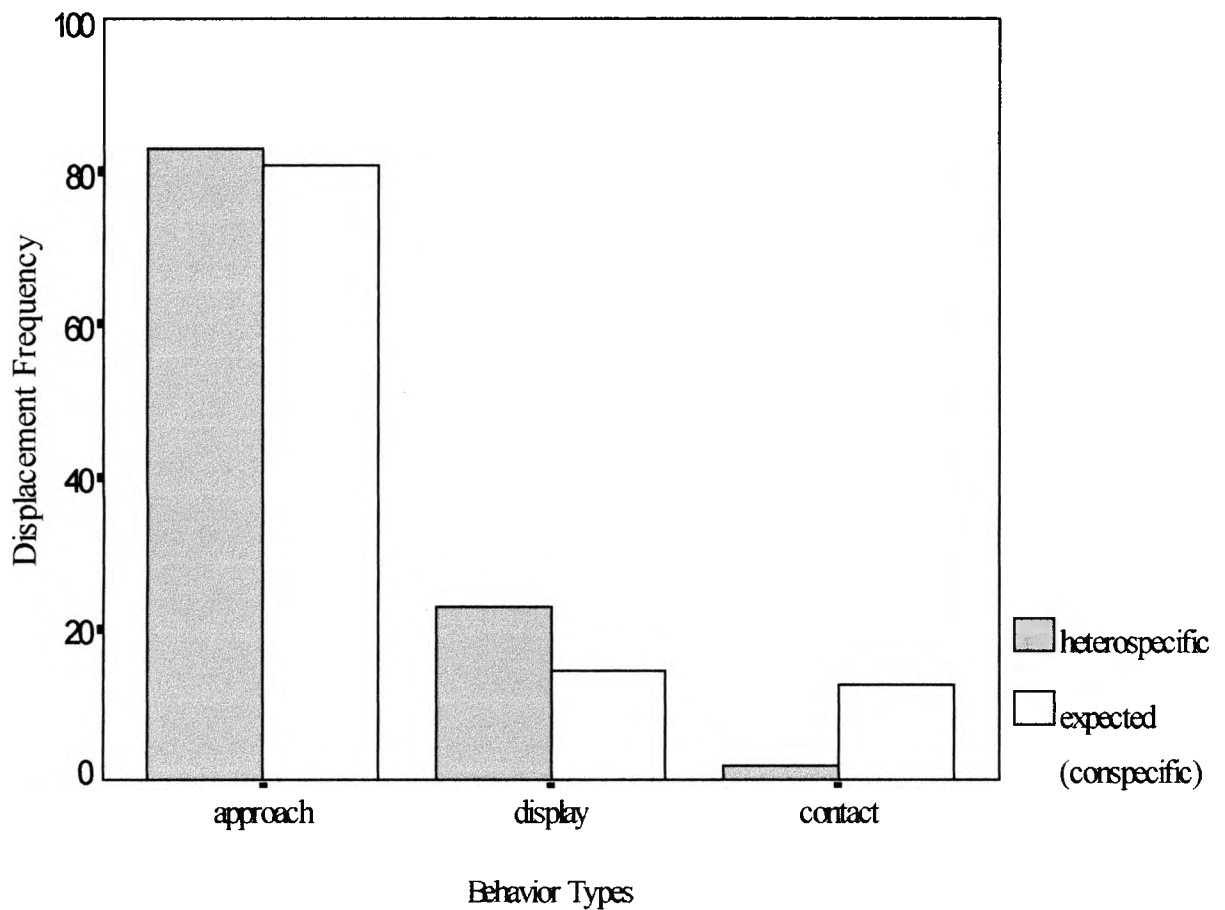


Figure 12. Distribution of heterospecific displacement behaviors compared to an expected distribution based on conspecific displacement behaviors in *Dama dama* males. The overall distribution of behaviors was not different between heterospecifics and conspecifics ($p < 0.10$). Contact level aggression alone, however, was more frequent between conspecifics ($p < 0.005$).

Table 4. Frequencies of conspecific and heterospecific *Axis axis* displacements based on behavioral intensity. Expected frequencies were based on the proportion of conspecific displacements in each category. *P*-values represent the probability that the distribution of displacement behaviors were the same between hetero- and conspecific encounters.

Interaction	Level of Behavior	Conspecific	Heterospecific	Expected Heterospecific Frequency
male vs. male	Approach/ Direct Attention	41	29	23.1
	Ritualized Display	31	19	17.5
	Contact/ Chase	15	1	8.4
male vs. yearling	Approach/ Direct Attention	13	16	15
	Ritualized Display	5	4	5.8
	Contact/ Chase	1	2	1.2
male vs. female	Approach/ Direct Attention	109	111	103.7
	Ritualized Display	44	41	41.9
	Contact/ Chase	15	8	14.4
yearling vs. yearling	Approach/ Direct Attention	1	1	0.2
	Ritualized Display	4	0	0.7
	Contact/ Chase	6	1	1.09
yearling vs. male	Approach/ Direct Attention	2	3	0.4
	Ritualized Display	10	0	2
	Contact/ Chase	2	0	0.6
yearling vs. female	Approach/ Direct Attention	12	13	11.6
	Ritualized Display	15	14	14.5
	Contact/ Chase	4	3	3.9
female vs. female	Non-Contact	18	31	19.3
	Contact	25	15	26.7*
female vs. male	Non-Contact	1	0	1
	Contact	0	0	0
female vs. yearling	Non-Contact	0	0	0
	Contact	0	1	0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 5. Frequencies of conspecific and heterospecific *Dama dama* displacements based on behavioral intensity. Expected frequencies were based on the proportion of conspecific displacements in each category. *P*-values represent the probability that the distribution of displacement behaviors were the same between hetero- and conspecific encounters.

Interaction	Level of Behavior	Conspecific	Heterospecific	Expected Heterospecific Frequency
male vs. male	Approach/ Direct Attention	83	83	80.8
	Ritualized Display	15	23	14.6
	Contact/ Chase	13	2	12.6
male vs. yearling	Approach/ Direct Attention	42	17	21
	Ritualized Display	7	8	3.5
	Contact/ Chase	3	1	1.5
male vs. female	Approach/ Direct Attention	179	75	73.8
	Ritualized Display	45	16	18.5
	Contact/ Chase	15	3	1.7
yearling vs. yearling	Approach/ Direct Attention	5	7	10
	Ritualized Display	0	3	0
	Contact/ Chase	0	0	0
yearling vs. male	Approach/ Direct Attention	4	12	24
	Ritualized Display	0	9	0
	Contact/ Chase	0	3	0***
yearling vs. female	Approach/ Direct Attention	38	13	22.4
	Ritualized Display	19	14	11.2
	Contact/ Chase	11	3	6.4
female vs. female	Non-Contact	28	19	19.2
	Contact	10	7	6.8
female vs. male	Non-Contact	0	2	0
	Contact	1	0	2
female vs. yearling	Non-Contact	0	0	0
	Contact	0	1	0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6. Chi-square comparison of the distribution of *Axis axis* interspecific contact and non-contact displacements to expected frequencies based on the distribution of intraspecific displacements by season.

Interaction	Level of Behavior	Fall		Winter		Spring		Summer	
		Inter	Intra	Inter	Intra	Inter	Intra	Inter	Intra
male > male	Non-Contact	1	9	4	30	14	15*	29	18
	Contact	0	0	0	7	0	6	1	1
male > yearling	Non-Contact	7	7	4	13	2	1	8	0
	Contact	0	0	1	3	0	0	0	0
male > female	Non-Contact	72	46	39	58	14	17*	31	33
	Contact	2	2	4	7	0	11	4	2
yearling > yearling	Non-Contact	1	2	0	3	0	0	0	0
	Contact	0	0	0	0	0	0	0	0
yearling > female	Non-Contact	16	9	19	13	0	1	0	0
	Contact	2	3	0	1	0	1	0	0
yearling > male	Non-Contact	0	1	0	10	2	0	1	0
	Contact	0	0	0	3	0	0	0	0
female > female	Non-Contact	7	2**	17	6***	3	7	4	3
	Contact	9	5	1	9	3	3	2	8

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 7. Chi-square comparison of the distribution of *Dama dama* interspecific contact and non-contact displacements to expected frequencies based on the distribution of intraspecific displacements by season. Spring comparison of female > female displacements was tested by Fisher's Exact Test because of low sample size.

Interaction	Level of Behavior	Fall		Winter		Spring		Summer	
		Inter	Intra	Inter	Intra	Inter	Intra	Inter	Intra
male > male	Non-Contact	31	18**	64	29*	8	6	11	26
	Contact	0	5	2	5	0	0	0	3
male > yearling	Non-Contact	11	12	14	26	0	7	0	0
	Contact	1	1	0	1	0	1	4	0
male > female	Non-Contact	34	109	55	67	11	12	8	33
	Contact	1	2	2	1	0	1	0	0
yearling > yearling	Non-Contact	1	0	9	3	0	4	0	0
	Contact	0	0	0	0	0	0	0	0
yearling > female	Non-Contact	10	23	17	34	0	6	0	2
	Contact	0	4	3	4	0	1	0	2
yearling > male	Non-Contact	1	0	13	0	9	1	0	0
	Contact	1	0	2	0	1	0	0	0
female > female	Non-Contact	12	13	4	9*	0	4	3	2
	Contact	3	9	3	1	1	0	0	0

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

a heterospecific yearling male (an approach). Conspecific displacement behaviors included one approach, three antler threats, and one parallel walk indicating that younger axis males expended more energy on displacements (Table 6). Male fallow yearlings, however, did not use contact level aggression to displace other yearlings. All conspecific displacements in this age class ($n = 5$) involved approaches, and did not differ substantially in distribution from the 10 observed heterospecific yearling displacements by year (Table 5) or season (Table 7). Yearling males of both species used contact level aggression in displacing females, but there was no difference between heterospecific and conspecific displacement behaviors by year (Tables 4 and 5) or by season (Tables 4 and 5). Male axis yearlings displaced axis adult males 14 times and fallow adult males three times; however, the distribution of heterospecific and conspecific displacement behaviors during the year were equal. The low number of displacements prevented seasonal testing; however, male axis yearlings displaced only adult males of both species in velvet or with recently shed antlers. For this reason, displacement of axis and fallow bucks occurred at different times of the year (Table 6). Male fallow yearlings displaced adult males 28 times. All but one of these displacements involved adults in velvet or with recently shed antlers. Fallow yearlings tended to exhibit more aggression toward axis adult males than fallow adult males when displacing them from food patches (Table 5). This relationship was seasonally tested in spring only, which did not differ from the annual relationship (Table 7).

Axis females displaced other females 89 times, with 46 of these interactions directed toward fallow females. Axis females showed more aggressiveness when displacing conspecific females throughout the year (Fig. 13), but at the seasonal level,

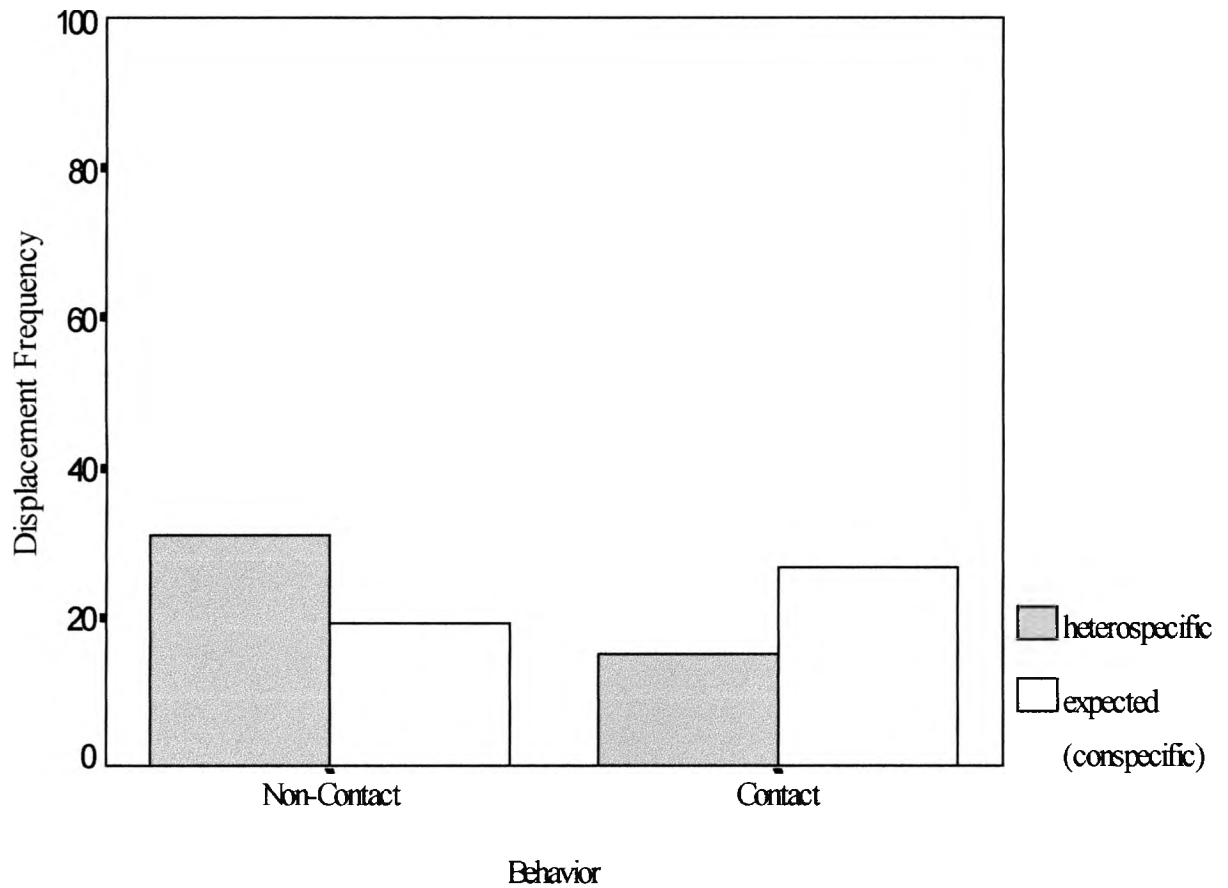


Figure 13. Distribution of heterospecific displacement behaviors compared to an expected distribution based on conspecific displacement behaviors in *Axis axis* females. The frequency of non-contact level aggression was not different between heterospecifics and conspecifics, however, contact level aggression was more frequent between conspecifics ($p < 0.05$).

axis does were significantly more aggressive toward conspecifics only in fall and winter (Table 4). Axis females rarely displaced male adults or yearlings of either species. An axis doe displaced a fallow yearling in hard antler by biting him once. An axis doe displaced an axis buck in velvet by an approach.

Fallow females displaced other females 64 times, with 26 interactions directed toward axis females. Fallow females equally displaced females of both species ($\chi^2 = 0.065$, d.f. = 1, $p = 0.7986$), but in winter they displaced axis does by contact more often than would be expected for conspecific displacements (Table 7). Fallow females rarely displaced male adults or yearlings of either species. Fallow females displaced a velvet-antlered axis yearling male and a hard-antlered fallow buck by biting. Fallow does displaced two velvet-antlered axis bucks by approaches.

Fallow/Axis Reproductive Cycles

Census data provided a measure of the reproductive cycles of both deer species for comparison to dominance patterns at food patches. I observed axis herds 1336 times and fallow herds 1757 times during the study. The estimated male: female sex ratio for fallow deer was 1:1.55 (males : females). The estimated male: female sex ratio for axis deer was 1:1.37. Interspecies associations were more common at food patches than among herds within the ranch. Herds of axis and fallow deer did not associate throughout the year, although approximately 40% of all axis and fallow herds occurred within 10 m of another species on the ranch (Table 8).

The percentage of mixed axis herds ranged from 35.9% in August 1999 to 15.2% in August 2000, with no discernable increase in one particular season. The major rutting

Table 8. Census route association indices for *Axis axis* and *Dama dama* by season and year. Axis and fallow herds whose outermost members were within 10 m of each other were considered in association. In addition, the percentage of herds observed within 10 m of any other species (including axis/fallow deer) are listed. Though axis and fallow herds were commonly in association with some species on the ranch (37-40% of sightings annually), association between axis and fallow deer was low, with little seasonal variation.

Season	axis/fallow association index	Axis % sightings any spp	Fallow % sightings any spp.
Fall	0.07	39	35
Winter	0.09	41	38
Spring	0.11	53	41
Summer	0.05	30	33
Annual	0.08	40	37

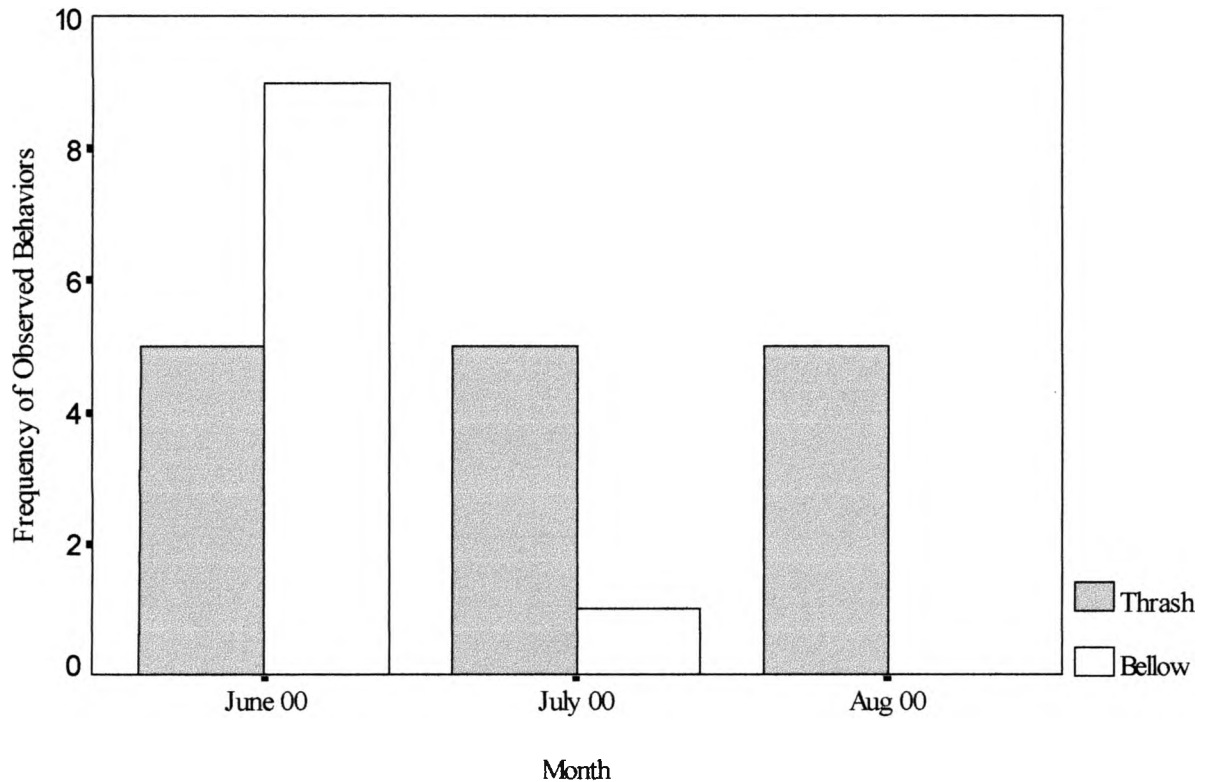


Figure 14. Frequency of thrashes and bellows of *Axis axis* males in 20 minute observation sessions at the Double D Ranch, Bastrop County, Texas. Thrashing of vegetation and bellowing occurred only from June to August 2000 indicating rutting behavior peaked in these months. Frequency of thrashes occurred equally in all three months while frequency of bellows peaked the first month they were observed and subsequently declined.

period for axis males occurred in June and July (Fig. 14). Mixed fallow herds range from 34.4% in October, 1999 to 5% in July, 2000, with the occurrence of mixed herds peaking in autumn, 1999. The percentage of fallow harems peaked in October, 1999 (Fig. 15).

Hard-antlered axis males were seen in all 16 months of census surveying, but the majority carried hard antlers during summer. Adult fallow bucks began shedding velvet in August and finished dropping antlers in April (Fig. 16). The percentage of hard-antlered deer attending food patches per month correlated with the percentage of the population in hard antler per month for axis deer ($r_s = 0.9157, p < 0.001$) and fallow deer ($r_s = 0.9610, p < 0.001$).

The fallow buck antler cycle correlated with displacements between interspecific males. The increase of axis deer in velvet was correlated with increased conspecific encounters (Table 9). Increases in the number of fallow or axis males attending food patches was associated with increases in displacements of those males. Increases in the number of males compared to females was also associated with increases in axis displacements of fallow bucks (Table 9). These correlations with increases in the number of deer present related to the calculation of displacement scores, and therefore, should be suspect. This is especially true of interspecific displacements, which would be most affected. The ratio of winners to losers between conspecific dyads will always be one, because the number of winners and losers will always be the same. Heterospecific displacement scores will usually be calculated by a number greater or less than one, because the number of winners and losers will usually differ, thus, the frequency of displacements in these types of dyads will be more greatly altered by the number of

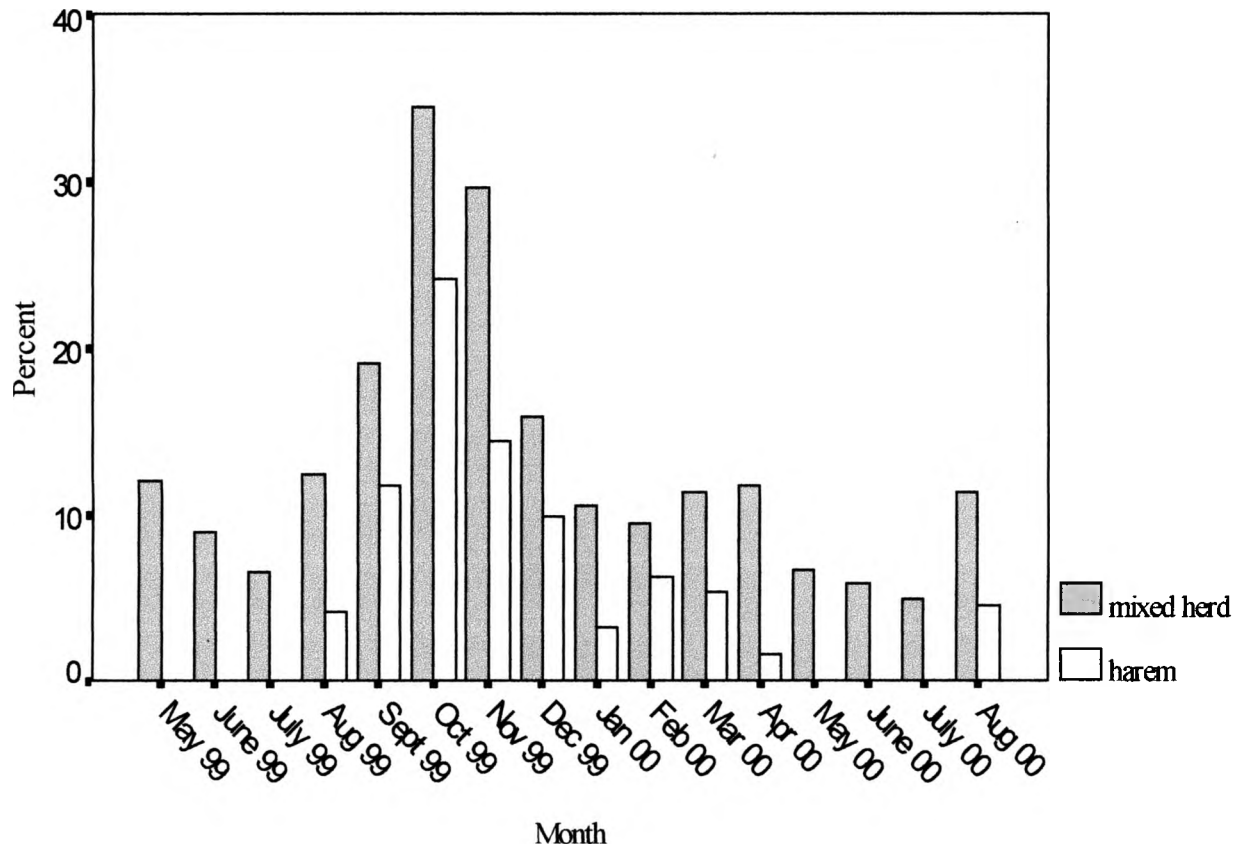


Figure 15. Monthly percentage of mixed *Dama dama* herds and harems observed on census routes at the Double D Ranch, Bastrop County, Texas. Distributions of both variables indicate a fall rut that peaks in October. The percent frequency of mixed herds (males and females) peaked from September to November 1999, with the percent frequency of fallow harems (1 adult male and ≥ 1 female) peaking in October 1999.

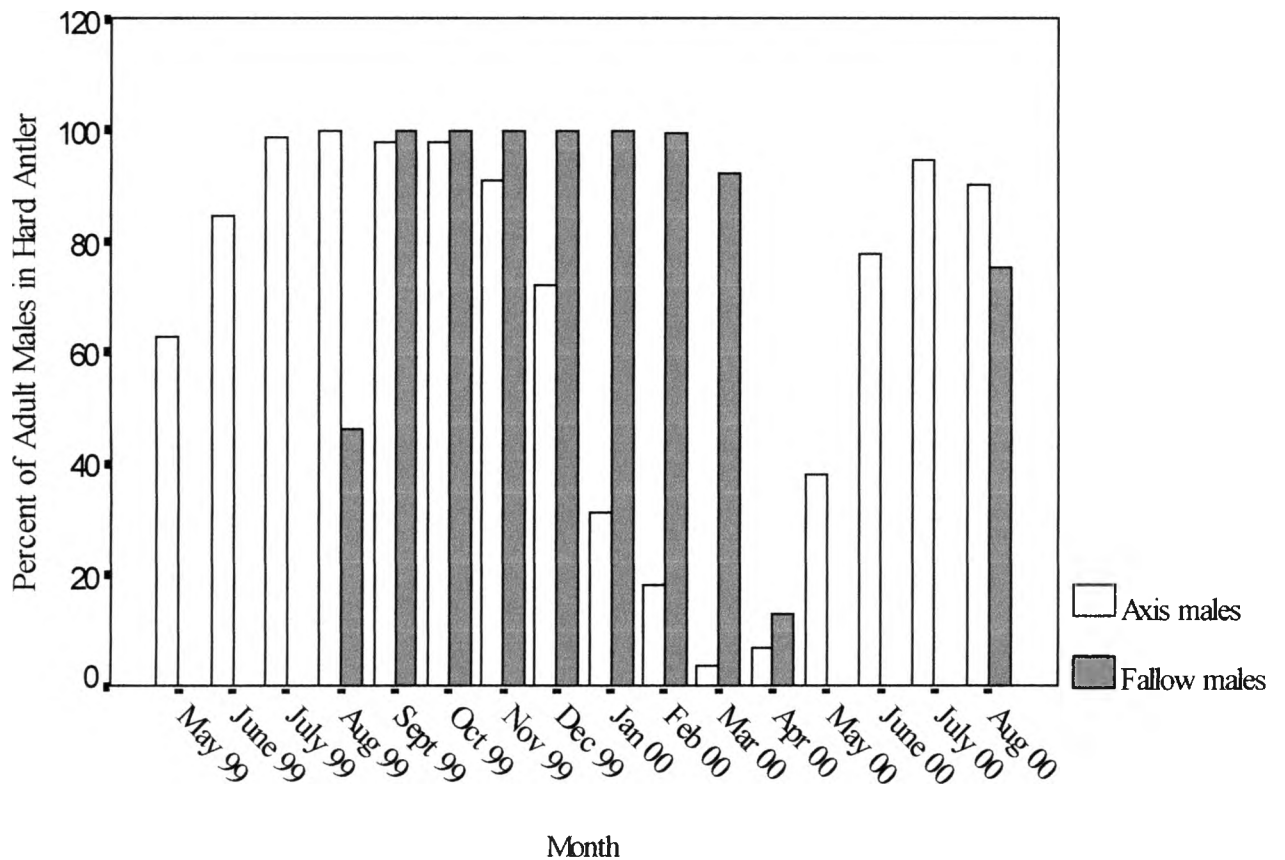


Figure 16. Monthly percentage of *Axis axis* and *Dama dama* males observed in hard antler on census routes at the Double D Ranch, Bastrop County, Texas. The distributions of percentage in hard antler indicate offset antler cycles and rutting periods between these species.

Table 9. Spearman correlation coefficients between displacement score values for male dyads and species sex ratio, number of males, and percent of males in hard antler at patches. The symbol > indicates a displacement interaction in which the individual on the open end is the actor.

Patch Characteristics	axis male >		fallow male >	
	axis male	fallow male	axis male	fallow male
percent hard antler axis at patches	-0.4267***	-0.0532	-0.1474	0.0306
percent hard antler fallow at patches	0.139	-0.6078***	0.3079**	0.0706
# axis males at patches	0.4912***	0.1662	0.4081***	0.1462
# fallow males at patches	-0.0718	0.2227*	0.0919	0.3309*
axis sex ratio	0.2803	0.4482***	0.1134	0.0739
fallow sex ratio	0.0172	0.3163**	-0.0002	0.1313

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

attendees of either species

Parturition times were similar for both species. The first observation of axis fawns (< 2 month old) was recorded on 4 January 2000. I continued to see axis fawns until 3 July. The first observation of fallow fawns occurred on 6 June 2000 and continued to 10 July (Fig. 17). The gestation period for axis deer ranges from 210 to 238 days (Mungall and Sheffield 1994). Axis fawn sightings were bimodally distributed indicating that matings may have extended into October of the previous year. The gestation period for fallow deer lasts 230 days (Mungall and Sheffield 1994), which indicates that the peak of the mating occurred in October, the same month with the highest percentage of harems.

Displacements by female deer did not correlate with the frequency of occurrence of fawns, nor presumably, the increased energy demands of lactation. Fallow females displaced other deer with a greater frequency in fall (Table 10). Increases in the number of axis females attending food patches were correlated with increased displacement of axis females, but increased numbers of fallow females were correlated with increased fallow displacements of both axis and fallow does (Table 10). Similarly, as the ratio of axis females to axis males increased, displacements in all female dyads rose, while only fallow conspecific displacements increased as fallow females began to outnumber males (Table 10).

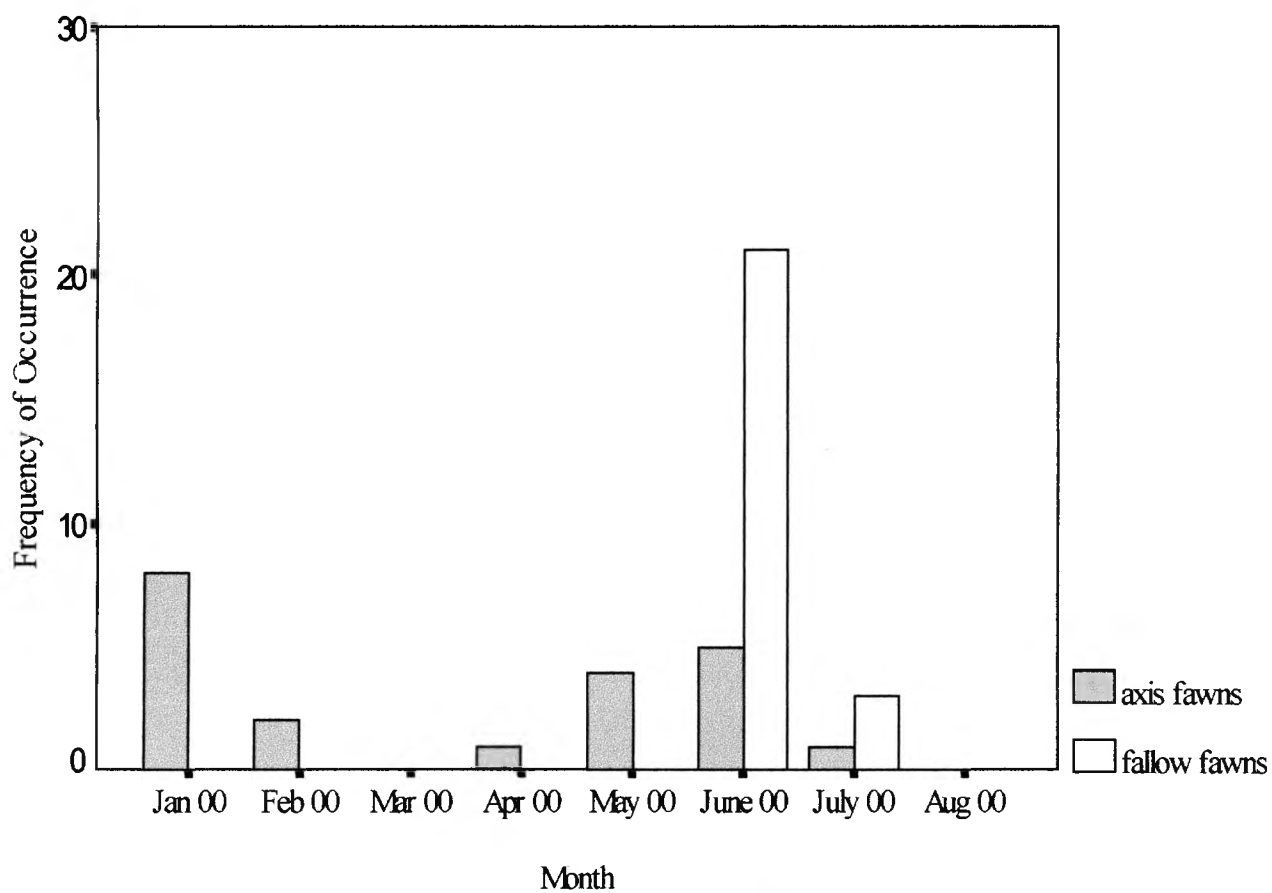


Figure 17. Monthly frequency of occurrence of fawns ≤ 2 months old for *Axis axis* and *Dama dama* deer on census routes at the Double D Ranch, Bastrop County, Texas. The distribution of observed fawns indicate a birthing peak in axis deer ranging from May to July 2000, and a fallow deer birthing peak for June and July 2000.

Table 10. Spearman correlation coefficients between displacement score values for female dyads and season, monthly fawn occurrence, species sex ratio at patches, and number of females at patches. Monthly fawn occurrence was based on census line data and was compared to a monthly median displacement score. The symbol > indicates a displacement interaction in which the individual on the open end is the actor.

Monthly fawn Occurrence & Patch Characteristics	axis female >		fallow female >	
	axis female	fallow female	axis female	fallow female
season	0.0044	-0.1176	-0.3033**	-0.3311**
monthly axis fawn occurrence	-0.0728	-0.5394	0.0001	-0.6179
monthly fallow fawn occurrence	-0.5401	-0.3889	-0.2546	-0.2546
# axis females	0.3646***	0.2002	0.2668*	0.1397
# fallow females	0.1081	0.0727	0.2164*	0.3490***
axis sex ratio	-0.2783*	-0.2276*	-0.3743***	-0.2246*
fallow sex ratio	-0.1022	-0.0146	-0.1535	-0.2960**

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

DISCUSSION

Annual Interspecies Dominance

In this study, interspecific dominance followed the same general patterns of intraspecific dominance. Adult males dominated yearling males and females, and yearlings in hard antler dominated females and adult males in velvet. Adult males in velvet were less likely to initiate a displacement than their hard-antlered counterparts, and having shed velvet gave an advantage to yearlings over adult males still in velvet. Few of these displacements occurred, and probably did not affect overall conspecific hierarchies. Age and sex are usually considered stronger indicators of dominance than the presence of antlers, but rank may temporarily fluctuate with differential antler loss (Appleby 1982, Suttie 1980, Espmark 1964). Differential antler loss will occur interspecifically, and might be of greater importance in these types of dyads.

No annual differences were indicated by displacement scores for either males or females within and between species. This suggests that no linear hierarchy exists between these species, which would afford greater access to nutrients. Interspecific hierarchies between vertebrate species, usually concerning birds and small mammals have been reported. Brown (1971) found a linear hierarchy between the chipmunk species *Eutamias dorsalis* and *E. umbrinus* based on the aggressiveness of the former. Although aggressiveness was considered a possible mechanism of competitive exclusion, a test of the hierarchy only occurred during summer. Heller (1971), however,

found aggressive dominance partly responsible for the distribution limits of four chipmunk species. Fisler (1977) demonstrated that, based on size, stable (year-round) hierarchies existed between taxonomically different species (Passerines, squirrels, quail, rabbits).

The lack of a stable hierarchy between axis and fallow deer and the relatively equal effort used to displace each other suggest that heterospecifics are not considered different from conspecifics in competition for food. Vankova *et al.* (1999) made a similar conclusion upon finding that food intake rates of white-tailed does (*Odocoileus virginianus*) were lowered in the presence of other deer regardless of species.

Seasonal Interspecies Dominance

Seasonal differences in the distribution of displacement scores existed between males and to some extent females. Axis bucks did not displace hard-antlered fallow deer, allowing fallow bucks priority access to food patches for the fall, winter, and part of spring. Conversely, after fallow males shed their antlers and the majority of axis bucks began shedding velvet, fallow bucks did not displace axis males during summer. Dominance appeared to be loosely associated with the breeding season of males. However, this pattern was not universal, as some fallow bucks in velvet displaced hard-antlered axis deer during summer, and hard-antlered axis males did not displace hard-antlered fallow bucks in fall as might be expected. Despite this, the percent of fallow males in hard antler attending food patches was correlated with the interspecific displacements of both species. The lack of correlation with the axis antler cycle is probably based on its relative aseasonality. Male deer displaced other males based on an

assessment process associated with the presence of hard antlers, some other related factor, or a combination of factors. While the correlation with the fallow antler cycle was significant, the test contained a great deal of residual error, meaning it may not be the best predictive factor of displacement. Other variable components of the breeding season (increase in testosterone production, differences in fighting experience, age, antler size, and intraspecies rank) may be better predictors of dyad outcomes. Clutton-Brock *et al.* (1979), for example, identified body weight as the most predictive factor of fighting success in red deer stags (*Cervus elaphus*). Unfortunately, because of the inter-relatedness of many of these variables, they are difficult to test separately. Antler condition is a good index of an individual buck's success. Barrette and Vandel (1986), for example, found that males with larger antlers than opponents initiated displacements more often than smaller antlered opponents. Perceived asymmetries in antler condition between bucks, are, therefore, a good indicator, and probably a primary factor of the assessment process between the two individuals.

Displacement scores were also related to the number of losing species at patches, which were used in their calculation. In the case of axis interspecific displacements, the sex ratios of both species were correlated with displacement scores. Although sex ratios would also be related to the calculation of displacement scores, one might infer that as the number of males increased in relation to females, axis bucks would more likely be forced into displacing males. Displacements occur between two individuals at any one time, however, so that numbers of deer seemed less important in the outcome of the interaction than the pertinent characteristics of the target individual.

Female patterns of interspecific dominance were less obvious. The seasonal distribution of displacement scores differed from the annual value in spring only. During

this period, axis does displaced conspecifics and heterospecifics with greater frequency than fallow does. The birthing season for axis deer extends from late winter to mid-spring (Ables 1977, Schaller 1967, Graf and Nichols 1966). This implies their increase in agonism is related to parturition and lactation as seen in mule deer (*Odocoileus hemionus*) (Koutnik 1981). However, I observed a bimodal distribution of fawns in this period, with fawns being observed in January and in late spring and early summer. This would indicate that the energy demands associated with lactation were less important in spring.

Aggression remained seasonally consistent in axis females; however, while fallow doe aggression exhibited a strong seasonal pattern. Agonism by fallow does decreased from a peak in fall to a low in summer. Axis does may have benefited in spring from a decrease in fallow doe aggression. Just as in axis males, however, aggression by axis females was correlated with both the number of target species at food patches and their sex ratios. Increases in aggression between axis and fallow does may also have resulted from a greater abundance of females at food patches.

Fallow females give birth in summer (Chapman and Chapman 1975). In this study, the frequency of fawns reached a maximum in summer. With high fawn numbers, displacement scores for fallow females were expected to increase, but they declined instead. Aggression by fallow does was greatest in fall and declined to a seasonal low in summer. This seasonal aggression may be an adaptation for this temperate zone species to increase nutrient intake for winter. Langbein and Putman (1992) found that winter weights of female fallow yearlings provided an important indicator of fawning success.

As with fallow males, correlations of aggression and displacement by fallow females had high residual values. Physical and behavioral characteristics not tested in this study may function as better predictors of displacement in fallow does. Dominance in does has been associated with both age and motherhood in a variety of cervids (Thouless and Guinness 1986, Koutnik 1981, Townsend and Bailey 1981, Espmark 1964), and may have been important in determining interspecific dominance.

Displacement Intensity

With the exception of contact level displacements, the amount of effort deer invested in displacement of other deer did not vary between and within species. Contact level displacements were the most aggressive and primarily used on conspecifics. This was true regardless of season with the exception of male fallow yearlings and fallow does. When displacing adult males, male fallow yearlings escalated their behavior to contact level displacements more often toward axis deer in velvet throughout the year. In winter, adult fallow does escalated their behavior more than expected against axis does. These data generally support the prediction made by Parker (1974) that escalation more likely occurs between evenly matched opponents. Conspecific seasonal changes in body size and antler development tend to be synchronous, even in axis deer. In heterospecifics, these features are less likely to be in synchrony. For this reason, asymmetries between species would be more pronounced than within species, reducing the need for escalation. These findings also argue against the presence of a long-term or seasonal hierarchy between these species. Neither axis nor fallow deer were required to escalate against heterospecifics beyond the aggressiveness they demonstrated toward members of their own species. Nor was one species typically required to expend greater

effort in the form of more aggressive behaviors in order to displace the other species. Females were the exception to this standard in fall and winter. During fall, axis deer spent greater energy displacing fallow; and during spring, fallow deer spent greater energy displacing axis deer. This implies that males and females invoke different mechanisms when deciding whether to escalate aggression or not. Males assess possible opponents for asymmetries in resource holding abilities, and thus may lower the probability of escalation by not attempting to displace those opponents they may have to escalate against. In the case of females, seasonal changes in energy requirements may affect escalation decisions. The fallow lactation requirements and their need to put on winter weight in fall may have made fallow does more aggressive or tenacious resource holders, requiring axis females to spend more effort displacing them. Likewise, the increased lactation requirements due to winter births in axis deer, may have forced fallow females to spend greater effort displacing axis does.

CONCLUSIONS

Priority of access to resources between deer species depends on factors similar to those seen within species. Bucks were displaced differentially based on antler development, suggesting that males assessed patch holders for asymmetries in overall fighting ability before attempting to oust them from their position. Does were displaced based on seasonal differences in aggression. These patterns in males and females agree with theoretical models of cost of fighting versus resource value, in which organisms are expected to increase aggression in relation to the value of the resource disputed and the probability of injury to themselves (Enquist and Leimar 1983, Clutton-Brock *et al.* 1979). Such an assessment process in conjunction with the offset breeding seasons of fallow and axis deer resulted in seasonal hierarchies.

Annual and seasonal interspecific dominance at food patches suggests that food intake is greater for hard antlered males than females, yearlings, and males in velvet. Thouless (1990) found that in red deer, subordinate hind bite rates decreased with increasing proximity to dominant hinds. Similarly, Vankova *et al.* (1999) found that white-tailed does decreased intake rates in the presence of heterospecifics and conspecifics, as opposed to feeding alone. However, subordinate deer may adopt strategies to maximize intake in the presence of dominants (Schmidt and Seivwright 1997). It remains unclear, then, the degree to which subordinates are affected by behavioral interactions at supplemental feeding sites in terms of actual food acquisition. While the degree of effect may be unknown, this study indicates that supplemental

feeding regimes may benefit only high ranking classes of deer. In addition, negative intraspecific dominance effects on subordinate deer would be compounded by interspecific dominance effects.

Association indices between axis and fallow deer on the Double D Ranch were low, indicating possible competitive interaction. While behavioral interaction may play an initial role in this separation, low association would also lower the rate of contest competition. Indeed, behavioral interactions between cervid species are typically low (Vankova *et al.* 1999, Bartos *et al.* in press). In an extreme example, Berger (1985) recorded 28 interspecies interactions between horses (*Equus caballus*), bighorn sheep (*Ovis canadensis*), pronghorn antelope (*Antilocapra americana*) and mule deer in 9000 hours of observation on the Great Basin Desert.

Heterospecific aggression, though qualitatively apparent, may not occur frequently enough to affect population dynamics except in situations of high density and/or patchy food distributions. Unfortunately, in Texas and particularly on the Edwards Plateau, these conditions often coexist. Increasing exotic populations on overgrazed rangeland with frequent summer drought conditions serves to increase the value of highly nutritious forage. Individual fitness differences within sympatric deer populations are more likely to be affected under these parameters. Dominant individuals may be able to hold high quality forage areas differentially, monopolizing prime habitat for extended periods, thereby affecting members of multiple species and herds. Bartos *et al.* (in press) reported some cervids avoided joining other species on pastures, and changed feeding rates when joined by other herds, regardless of species. Appleby (1980) reported that high ranking stags monopolized fertilized grass patches and displaced other stags from preferred forage sites. Colgrave (1994) suggested that

asymmetries in competitive ability and fighting ability may lead to differing strategies for obtaining food. In the case of deer, individuals in velvet and females may increase bite rates in the presence of other deer or avoid optimal habitat held by hard-antlered males in favor of other pastures. Conversely, hard-antlered males may join other deer on optimal habitat, hold high nutrient patches of forage, and maintain steady bite rates with or without the presence of lower ranking deer.

MANAGEMENT IMPLICATIONS

Exotic species will likely continue to be stocked worldwide in habitats with ecologically equivalent species with which they must theoretically compete. As exotic populations increase and available habitat and niche space decrease, the impact of contest competition will become increasingly important to wildlife managers. Both contest and scramble competition will be instrumental in determining the distribution of populations and their use of available habitat for both exotic and native deer. Henke *et al.* (1988) reported that sika deer, fallow deer, and blackbuck antelope were better able to utilize grass diets than white-tailed deer, giving them a competitive advantage in overgrazed habitat. Furthermore, Baccus *et al.* (1983) reported that sika deer populations can outcompete white-tailed deer populations in high fenced pastures. This study and others (Bartos *et al.* in press, Vankova *et al.* 1999, Bartos *et al.* 1996), indicates that behavioral interactions may contribute to defining local habitat use. Continued study of both competition types is required to determine the importance of each relative to the other in order to manage for healthy native populations and maintain the economic benefits of the exotic populations already in the state.

The use of supplemental feed to maintain high deer densities or produce large antler sizes is common on Texas game ranches, but may only benefit the hard-antlered adult males in a given area, regardless of species. In order to increase supplemental feed use by other age and sex classes, game managers should disperse supplemental feed widely to reduce its defensibility. Large amounts of supplemental feed should be

deposited, allowing subordinate animals to eat leftover feed after dominant animals have finished using it. Game managers wishing to add species to their ranches should be aware that doing so will compound multispecies dominance interactions and may put native species at a competitive disadvantage. White-tailed deer populations may suffer a decline over the long-term on high-fenced ranches stocked with multiple species.

If one assumes high-quality forage exists in discrete patches, this study indicates that hard-antlered stags will monopolize them, regardless of species. In Texas, forage is most limiting in summer. Axis bucks are dominant during this period, and are most likely to monopolize supplemental feed and natural forage patches. Interspecies dominance may also result in increased foraging times for low ranking sex and age groups as dominant members of multiple species will have right of access to the best and most easily found forage patches. Managers may offset this by increasing the spread of high quality forage through planting.

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