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Intraspecific temporal resource partitioning at white-tailed deer feeding sites

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Abstract

Individuals may reduce competition by temporally partitioning their use of a shared resource. Behavioral differences between sexes in ungulates may encourage segregation as individuals attempt to avoid antagonistic interactions. However, dominant sex and age groups may reduce subordinates' access to food resources, regardless of the subordinate's sex. We hypothesized that white-tailed deer *Odocoileus virginianus* temporally segregated at supplemental feeding sites based on social rank (subordinate: yearling males and adult females; dominant: adult males) and that segregation was affected by phase of the breeding season and diel cycle. If deer temporally segregate according to social rank, we predicted that the resulting activity patterns would manifest in one social class being relatively more susceptible to hunter-induced mortality. We used a multi-state modeling approach to quantify temporal segregation and calculated the probability that a feeding site was in a particular state during diurnal and nocturnal hours during the 3 phases of the breeding season. We determined that transition probabilities differed by season and diel cycle and dominant and subordinate social classes clearly avoided each other, with < 1% co-occurrence at feeding sites. During the pre-breeding season, the probability of a subordinate being present during diurnal hours was 3.0x more likely than a dominant being present, but did not differ during nocturnal hours. There was no difference for dominants and subordinates during diurnal or nocturnal hours during the breeding season. In the post-breeding season, subordinates were 1.7x more likely to occur at the feeding site than a dominant during diurnal hours but they did not differ during nocturnal hours. Our results indicate that dominance status influences temporal segregation at feeding sites and is affected by the phase of the breeding season. Therefore, the resulting activity patterns may increase subordinates' risk to human predation during the pre-breeding and post-breeding seasons.

Key words: competition, multi-state modeling predation risk, supplemental feeding sites, intraspecific temporal resource portioning, white-tailed deer

Individuals may reduce competition by partitioning resources temporally and spatially (Schoener 1971; Ziv et al. 1993; Howerton and Mench 2014). Temporal resource partitioning, in particular, can be vital to the coexistence of species, or individuals, that share a common resource (Ziv et al. 1993). Mechanisms driving temporal resource partitioning are similar for inter- and intra-specific competition. Sex-specific behavioral differences in ungulate resource use increases

segregation as individuals attempt to avoid antagonistic interactions (Bowyer 2004). However, interference competition from dominant sex-age classes may reduce subordinates' access to food resources, regardless of sex (Appleby 1980; McGhee and Baccus 2006; Donohue et al. 2013). For example, subordinate male red deer *Cervus elaphus* may avoid using feeding sites when patch profitability does not outweigh the costs of agonistic interactions with dominant males (Schmidt et al. 1998). Additionally, Grenier et al. (1999) reported that female and fawn white-tailed deer *Odocoileus virginianus* had greater access to food when adult males were not present.

Older, larger ungulate males are generally dominant over smaller males and females (Grenier et al. 1999; Côté 2000; Donohue et al. 2013), but dominance hierarchies are seasonally dynamic (Grovenburg et al. 2009; Koutnik 1981). *Odocoileus* spp. exhibit marked sexual segregation outside of the breeding season with males forming loose aggregations that consist of various age classes (Hirth 1977; Lagory 1986; Miller and Conner 2005). Female groups consist of a matriarchal female, multiple generations of her female offspring, and pre-dispersal males (Hirth 1977; Lagory 1986). Male dispersal typically occurs in their first spring or second autumn (Rosenberry et al. 1999). Therefore, during autumn, yearling males may be solitary or associate with either matrilineal or all-male groups. Regardless of their social affiliation, yearling males are competitively disadvantaged compared to adult males (Donohue et al. 2013).

Competitive asymmetries are common at concentrated resources (Donázar et al. 1999; Donohue et al. 2013; Milner et al. 2014). It is possible that in populations with clear dominance hierarchies, competition drives temporal resource partitioning. Furthermore, if competitors temporally segregate their use of a shared resource, then subordinates may use the resource only when dominants are absent. Resulting activity patterns at the resource may enhance or diminish susceptibility to predation, depending on the suite of predators and their associated activity cycle.

Temporal resource partitioning has been studied in sympatric species of mammals (Kronfeld-Schor and Dayan 1999, Jacamo et al. 2004, Adams and Thibault 2006) and within cohorts of the same species (Taillon and Côté 2006, Taillon and Côté 2007). However, the effect of social rank on intraspecific temporal resource partitioning across sex-age classes has not been investigated in ungulates. We hypothesized that white-tailed deer would temporally segregate use of supplemental feed sites based on competitive status whereby adult females and yearling males would avoid encounters with adult males. Moreover, if we observed temporal resource partitioning based on competitive status, we hypothesized that activity patterns at the feeding sites would manifest in one social group being more at risk to hunter-induced mortality. We tested these hypotheses in a population of white-tailed deer offered supplemental feed during the hunting season.

Materials and Methods

Study area

 We conducted this study on a 1,619-ha property in Harris County, GA, USA (32.8023°N, −84.9049°W). Pine stands made up approximately 983 ha (61%) of the land cover and were comprised primarily of loblolly *Pinus taeda* and shortleaf pine *P. echinata*. Hardwood stands constituted approximately 582 ha (36%) of the study site and were dominated by oak (*Quercus* spp.), hickory (*Carya* spp.), tulip-poplar *Liriodendron tulipifera*, and sweetgum *Liquidambar styraciflua*. Open areas included pasture, fallow fields, row crops, and cultivated wildlife openings.

White-tailed deer hunting occurred on the property from the 13 September–15 Janaury, 2013 and 14 September–15 January, 2014. The property received light hunting pressure and approximately 10 deer (< 1 deer per 160 ha) were harvested annually. Hunter effort data indicated that on average, one hunt (i.e., a single hunter from a fixed location) occurred every 2 days. Camera surveys (Jacobson et al. 1997) conducted in August 2013 and 2014 estimated the deer density was 0.16 and 0.19 deer per hectare, respectively. The buck:doe ratio was approximately 1:1.1 in both years. Hunters typically harvested only mature males and adult females. Although hunting pressure on the site was relatively low during our study period, the site had been hunted for decades under varying harvest criteria and deer were not naïve to the threat of human predation.

Non-human predators on the site included bobcats *Lynx rufus* and coyotes *Canis latrans*. Although coyotes can affect fawn survival in some regions (Ballard 2011), they are not effective predators of adult deer in the southeastern United States (Chitwood et al. 2014). Where bobcats are sympatric with coyotes, food habit studies indicate that bobcats are not responsible for significant direct mortality on adult deer (VanGilder 2008).

Study Design

We established 16 feeding sites across the study site and used shelled corn as supplemental forage. Hunters were allowed to hunt at feeding sites and feed was provided *ad libitum* throughout the duration of the study, which began > 2 weeks prior to data collection to allow deer to acclimate to the feeding sites. From 13 September − 3 January in 2013 and 2014, we used infrared cameras (Reconyx Hyperfire 550, Holmen, WI, USA) to observe visitation rates. We mounted cameras to a tree or post 3 – 4 m from the feed site and approximately 75 cm from ground level. Cameras were triggered by motion and recorded photographs 24 hrs per day, with a 5-minute delay between successive photographs. We assigned each deer observation to a sex-age class [adult male (≥ 2.5 years-old), yearling male (1.5 years-old), and adult female (≥ 1.5 years-old)] based on antler and body morphology (Richards and Brothers 2003), and recorded the time and date of the photograph. Adult male dominance at concentrated resources is well documented in white-tailed deer (Ozoga 1972, Weeks 1978, Donohue et al. 2013). Because both yearling males and adult females are subordinate to adult males during autumn, we pooled their observations. We excluded photographs when the sex-age class for all individuals in the photograph could not be determined.

Although adult males are dominant throughout autumn and early winter, social dynamics and the frequency of aggressive interactions change relative to the breeding season (Hirth 1977). Furthermore, physiological and behavioral changes related to breeding activity occur in males and could affect the degree of temporal partitioning. Therefore, we divided the study period into pre-breeding, breeding, and post-breeding seasons based on conception data from the study site (Stickles et al. 2015): 1) Pre-breeding -- weeks 1−6 (13 September − 25 October); 2) Breeding -- weeks 7−11 (26 October − 27 November); and 3) Post-breeding -- weeks 12−16 (28 November − 3 January).

We sub-sampled photographs obtained for three days (Monday, Tuesday, and Wednesday) of each week due to the large number of photographs recorded at feeding sites. We binned each observation of a deer at a feeding site by hour of the day (0−23). We divided the diel cycle into diurnal and nocturnal hours based on legal hunting hours to determine the relative exposure of each social group to human predators. We used the hours in which legal hunting began and ended for our delineation of diurnal and nocturnal hours.

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Models

To test our hypothesis that deer temporally segregated use of the feeding site based on social rank, we used a multi-state modeling approach. In any given hour, the feeding site could have been in State 1 (no deer present), State 2 (subordinate present), State 3 (dominant present), or State 4 (both a dominant and subordinate present). We used all photographs of deer recorded during each hour to determine the state of the feeder, and did not consider photographs of other species in our analyses. If all of the photos collected during a given hour at a particular feeding site were of adult males and we collected no photos of adult females or yearling males during that hour, the state of the feeding site for that hour was State 3 (dominant present). Likewise, if an adult female and an adult male were photographed during a given hour at a particular feeding site, the state of the feeding site for that hour was State 4 (both a subordinate and a dominant present).

To quantify any potential temporal segregation between dominants and subordinates (segregation model), we used package 'msm' (Jackson 2011) for R version 3.1.2 (R Core Team 2014) to calculate hazard ratios (HRs) and transition probabilities . Because feeding sites were available to all deer during all hours, we considered all transitions equally possible (see Figure 1 for transition diagram). Therefore, we assigned each transition an initial value of 0.25 in the transition intensity matrix. We estimated hazard ratios and transition probabilities by season (pre-breed, breed, and post-breed) and time-of-day (diurnal or nocturnal), and used 'state' as the response variable in our model. Hazard ratio values of 1 indicate that the transition probabilities did not differ according to season or time-of-day (Jackson 2011).

In addition, we estimated probabilities for going from one state at time t to a different state at time $t+1$ during each season and period. Transition probabilities from state 1 (no deer present) at time t to any other state at time $t+1$ are not affected by the presence of another social class occurring at a feeding site. Therefore, transition probabilities from state 1 (no deer present) to any other state are predicted to be equal (see Prediction 1, Table 1). Furthermore, if the presence of either social class at time t does not affect the probability of another social class occurring at the feeding site at time $t+1$, we predict the transition probability from one social class to another to be equal to the probability of transitioning to state 1 (see Prediction 2, Table 1).

To determine if temporal segregation between dominants and subordinates manifested in differential arrival times and use (i.e. nocturnal vs. diurnal) , we implemented Markov chain Monte Carlo (MCMC) routines to fit multinomial response (states 1–4) generalized linear mixed models in package 'MCMCglmm' (Hadfield 2010; hereafter; Diel Model). We modeled the response (state) by season, diel phase (diurnal or nocturnal hours), and their interactions. We treated the feeding site as a random effect.

Results

Camera trapping effort was 375, 411, and 402 camera days for the pre-breeding, breeding, and post-breeding seasons, respectively. We collected 6,994 photographs containing images of 8,469 white-tailed deer for which we could assign a sex-age class, and excluded fawns from our analyses. We recorded a total of 3,192 adult male (47.1%), 1,365 yearling male (20.1%), and 2,225 (32.8%) adult female images. During the pre-breeding season, cameras collected 1,164 (48.2%) adult male, 399 (16.5%) yearling male, and 850 (35.2%) adult female images. We observed a decline in images of all sex-age classes during the breeding season with 459 (36.4) adult male, 177 (14.0%) yearling male, and 625 (49.6%) adult female images captured at feeding sites. During the post-breeding season, cameras collected 1,569 (50.5%) adult male, 789 (25.4%) yearling male, and 750 (24.1%) adult female images. Our hourly bins resulted in 18,432 total state

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occurrences (Table 2) with only 195 occasions of the feeding site being in state 4. Furthermore, we detected only 54 co-occurrences of subordinates and dominants in the same photograph.

Hazard ratios from the segregation model indicated that transition probabilities varied according to season and the diel cycle. During the pre-breeding season, transitions 1–2 (HR, 95% confidence interval; HR =1.61, CI = 1.25–2.08) and 1–3 (HR = 1.77, CI = 1.39–2.25) were more likely to occur than during the breeding season (Table 3). Transition 3–1 was less likely to occur in the pre-breeding (HR = 0.78, CI= 0.61–0.98) and post-breeding (HR = 0.75, CI = 0.60–0.94) seasons than in the breeding season (Tables 3 and 4). Compared to the breeding season, transition probabilities for transitions 1–2 (HR = 2.91, CI = 2.28–3.71), 1–3 (HR = 2.93, CI = 2.32–3.68), and 1–4 (HR = 6.35, CI = 3.52–11.45) were greater during the post-breeding season (Table 4). During diurnal hours, transition probabilities for transitions 1–2 (HR = 0.69, CI = 0.58–0.83), 1–3 (HR= 0.31, CI = 0.27–0.38), and 1–4 (HR = 0.48, CI = 0.33–0.70) were less likely to occur than at night (Table 5).

The probabilities for the next state to occur revealed marked temporal segregation at individual feeding sites. For Prediction 1 (Table 1), transition probabilities for transitions 1–2 and 1–3 were greater than 1–4 during diurnal and nocturnal hours in all seasons (Figure 1). Interestingly, Transition probabilities for transition 1–2 were consistently greater than 1–3 during diurnal hours (Figure 1). During nocturnal hours, transition probabilities for transition 1–3 were greater than 1–2 during all seasons (Figure 1). For Prediction 2 (Table 1), transitions 2–1 and 3–1 were greater than transitions 2–3 and 3–2 in all seasons during both diurnal and nocturnal hours (Figure 2).

Results of the diel model indicated that the probability of the feeder being in a particular state differed by diel cycle and season (Table 6). During the pre-breeding season, the probability of a subordinate being present during day was $3.0x$ more likely than a dominant being present but did not differ at night (Figure 3). Additionally, the probability of an adult male being present at the feeder was $5.9x$ greater at night than day during the pre-breeding season (Figure 3). During the breeding season, there was no difference for dominants and subordinates during diurnal or nocturnal hours (Figure 3). In the post-breeding season, subordinates were $1.7x$ more likely to occur at the feeder than a dominant during diurnal hours but there was no difference during nocturnal hours (Figure 3).

Discussion

Animals can reduce competitive interactions for a shared resource through temporal resource partitioning (Alanärä et al. 2001). However, how animals segregate along the temporal niche axis has been the focus of few studies, particularly in mammals (Adams and Thibault 2006). In the present study, dominants and subordinates within the same species showed a clear pattern of avoidance of the opposing social class, with segregation varying according to season and the diel cycle.

Feeding site use was only similar for dominants and subordinates during the breeding season. However, feeding site use was also lowest for both groups during this season. Adult males increase diurnal movements from pre-breeding to breeding season (Tomberlin 2007; Webb et al. 2010) and it is during this time that males switch their focus from foraging to mate-searching behaviors (Beier and McCullough 1990; Tomberlin 2007). Furthermore, many adult male ungulates exhibit hypophagia during the breeding season (Warren et al. 1981; Chin and Brown 1984; Brivio et al. 2010) and visit feeding sites less than during the pre- and post-breeding seasons (Ozoga and Verme 1982). As mating activities are prioritized over foraging during the breeding season, the breeding males' activity budget is directed away from foraging activity (Pelletier et al. 2009). Younger males, however, do not invest as heavily in breeding activities allowing them to place a higher priority on growth to improve future opportunities for mating (Mysterud et al. 2008;

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Foley et al. 2015). Consequently, they are not as hypophagic as adult males during the breeding season (Mysterud et al. 2008).

Why subordinates also decreased feeding site visitation during the breeding season is unclear. With the lack of dominants at the sites, subordinates had greater access to the supplemental feed, but did not use it as heavily during the breeding season. Although yearling males do not exhibit the same intensity of search behavior as adult males, they do engage in mate-searching (Foley et al. 2015). Moreover, peak dispersal of yearling males coincides with the breeding season (Rosenberry et al. 1999). Therefore, some yearling males present during pre-breeding may have emigrated from the site, while immigrating yearling males would be naive to the feeding site locations.

Adult females of many species are often harassed by breeding males (Clutton-Brock et al. 1992; Reale et al. 1996; Holand et al. 2006). Harassment can lead to poorer body condition (Holand et al. 2006) and even direct mortality (Reale et al. 1996). Therefore, spatially and temporally avoiding breeding males is beneficial for females when not in estrus, which may explain why feeding site use was lowest for females during the breeding season.

During the post-breeding season, males may be in poor physical condition, making abundant, high-energy food sources very profitable patches at which to forage. However, agonistic interactions are energetically expensive (Appleby 1980) and defending the feeding site from subordinates during this time would lessen the profitability of the resource. Likewise, testosterone levels are lower during the post-breeding season (Chin and Brown 1984; Miller et al. 1987) making aggressive behaviors less likely (Lincoln et al. 1972). Together, energy conservation and lowered aggression by adult males may explain why we observed less temporal segregation in the post-breeding season.

Dominance status clearly influenced temporal patterns in feeding site use. Adult male occurrences at the feeding sites were lower during diurnal periods, particularly during the pre-breeding season. The pattern of temporal partitioning whereby subordinates were more likely to occur at the feeding sites during diurnal hours has obvious implications for human-induced mortality. Although hunting pressure was relatively-low on our site, in most of the region hunting is responsible for the majority of deer mortality (Dusek et al. 1992), especially because most large carnivores have been extirpated. On our study site, predation risk from carnivores and hunters was low because hunting pressure was light and bobcats and coyotes are not efficient predators of adult deer. Previous research at the site demonstrated that no sex-age class altered vigilance levels at feeding sites according to the diel cycle (Stone et al. 2017). Therefore, deer may not have focused their anti-predator behaviors toward a specific predation threat.

Our study illustrates how patterns in temporal resource partitioning at feeding sites may influence relative risk to different sources of mortality. Subordinates used the shared resource at similar rates, but the pattern of temporal partitioning evidently would make subordinates more susceptible to human predation. Further research is needed to determine if an increase in hunting pressure acts to compress temporal partitioning at feeding sites and how the resulting temporal patterns affect predation risk for dominant and subordinate social classes.

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Table 1. Predictions, state transitions, and interpretation for our hypothesis that white-tailed deer would temporally segregate use of supplemental feed sites based on competitive status. If we observed that state transitions were equal, we interpreted the results to indicate that there was no temporal segregation.

Prediction	State Transitions	Interpretation
1[a]	1–2 = 1–3 = 1–4	No temporal segregation
2	2–3 = 2–1	
	3–2 = 3–1	No temporal segregation

[a]State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present,

State 4 = subordinate and dominant present

Table 2. Frequency of each state during nocturnal and diurnal hours of the pre-breeding, breeding, and post-breeding seasons. State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present. State

	Pre-breeding		Breeding		Post-breeding	
	Nocturnal	Diurnal	Nocturnal	Diurnal	Nocturnal	Diurnal
1	2560	3788	2487	3029	2299	2600
2	135	95	64	40	197	147
3	234	45	75	45	265	132
4	47	8	14	6	71	49

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Table 3. Hazard ratios (HR) and 95% confidence limits for transition probabilities at white-tailed deer supplemental feeding sites in Harris County, Georgia, USA (2013 – 2014) during the pre-breeding season (13 September − 25 October), as compared to the breeding season.

Transition[a]	HR	Lower	Upper
State 1 - State 2	1.61	1.25	2.08
State 1 - State 3	1.77	1.39	2.25
State 1 - State 4	1.87	0.97	3.63
State 2 - State 1	0.88	0.68	1.15
State 2 - State 3	0.65	0.25	1.70
State 2 - State 4	1.82	0.39	8.57
State 3 - State 1	0.78	0.61	0.98
State 3 - State 2	1.81	0.39	8.43
State 3 - State 4	2.23	0.48	10.30
State 4 - State 1	1.11	0.50	2.47
State 4 - State 2	0.80	0.25	2.62
State 4 - State 3	0.82	0.28	2.38

[a]State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present

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Table 4. Hazard ratios (HR) and 95% confidence limits for transition probabilities at white-tailed deer supplemental feeding sites in Harris County, Georgia, USA (2013 – 2014) during the post-breeding season (28 November − 3 January) as compared to the breeding season.

Transition[a]	HR	Lower	Upper
State 1 - State 2	2.91	2.28	3.71
State 1 - State 3	2.93	2.32	3.68
State 1 - State 4	6.35	3.52	11.45
State 2 - State 1	0.86	0.67	1.10
State 2 - State 3	1.26	0.55	2.88
State 2 - State 4	2.44	0.56	10.64
State 3 - State 1	0.75	0.60	0.94
State 3 - State 2	3.60	0.85	15.23
State 3 - State 4	2.60	0.60	11.26
State 4 - State 1	1.33	0.64	2.78
State 4 - State 2	0.97	0.33	2.82
State 4 - State 3	0.69	0.26	1.83

[a]State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present

Table 5. Hazard ratios (HR) and 95% confidence limits for transition probabilities at white-tailed deer supplemental feeding sites in Harris County, Georgia, USA (2013 – 2014) during diurnal hours as compared to nocturnal hours.

Transition	HR	L	U
State 1 - State 2	0.69	0.58	0.83
State 1 - State 3	0.32	0.27	0.38
State 1 - State 4	0.48	0.33	0.70
State 2 - State 1	0.96	0.80	1.15
State 2 - State 3	0.89	0.49	1.62
State 2 - State 4	0.86	0.39	1.90
State 3 - State 1	1.11	0.93	1.33
State 3 - State 2	0.71	0.32	1.58
State 3 - State 4	1.18	0.53	2.63
State 4 - State 1	0.87	0.55	1.36
State 4 - State 2	0.88	0.43	1.83
State 4 - State 3	1.19	0.59	2.39

[a]State 1 = no deer present, State 2 = subordinate present, State 3 = dominant present, State 4 = subordinate and dominant present

Table 6. Estimates from Markov chain Monte Carlo generalized linear mixed model predicting the probability of a supplemental feeding site being in 1 of 4 states during the pre-breeding, breeding, and post-breeding seasons during diurnal and nocturnal hours.

	Posterior Mean	Lower CI*	Upper CI*	pMCMC[#]
(Intercept)	-4.046	-4.242	-3.883	<0.001
state2:breed:diurnal[a]	-0.644	-0.828	-0.391	<0.001
state3:breed:diurnal	-0.944	-1.317	-0.553	<0.001
state4:breed:diurnal	-0.831	-1.081	-0.639	<0.001
state2:post:diurnal	1.010	0.861	1.165	<0.001
state3:post:diurnal	0.385	0.153	0.702	<0.001
state4:post:diurnal	-0.044	-0.163	0.132	0.454
state2:pre:diurnal	0.212	0.067	0.389	<0.001
state3:pre:diurnal	-1.097	-1.417	-0.752	<0.001
state4:pre:diurnal	-1.128	-1.318	-0.831	<0.001
state2:breed:nocturnal	0.112	-0.084	0.307	0.328
state3:breed:nocturnal	-0.170	-0.515	0.210	0.430
state4:breed:nocturnal	-0.694	-0.837	-0.559	<0.001
state2:post:nocturnal	1.433	1.242	1.589	<0.001
state3:post:nocturnal	1.302	1.047	1.620	<0.001
state4:post:nocturnal	0.418	0.204	0.657	<0.001
state2:pre:nocturnal	0.926	0.751	1.091	<0.001
state3:pre:nocturnal	1.052	0.875	1.266	<0.001

*Represent lower and upper 95% credibility intervals

[#]Number of simulated cases that are >0 or <0 corrected for number of MCMC samples

[a] State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present. Reference class is State 1.

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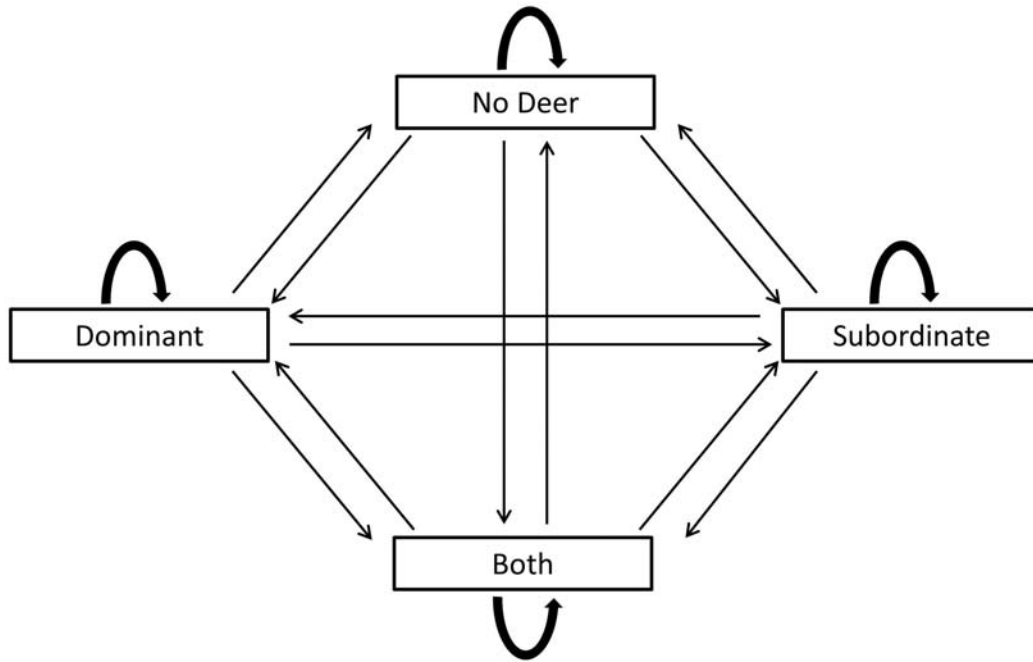
Figure 1. Transition diagram for multi-state model used to estimate probability of feeding sites transitioning from one state to another state, or the probability of the feeding site staying in the same state. There were 4 possible states (States 1–4) that a feeding site could be in during any given hour. State 1 = no deer present, State 2 = subordinate (adult females and yearling males) present, State 3 = dominant (adult males) present, and State 4 = subordinate and a dominant present.
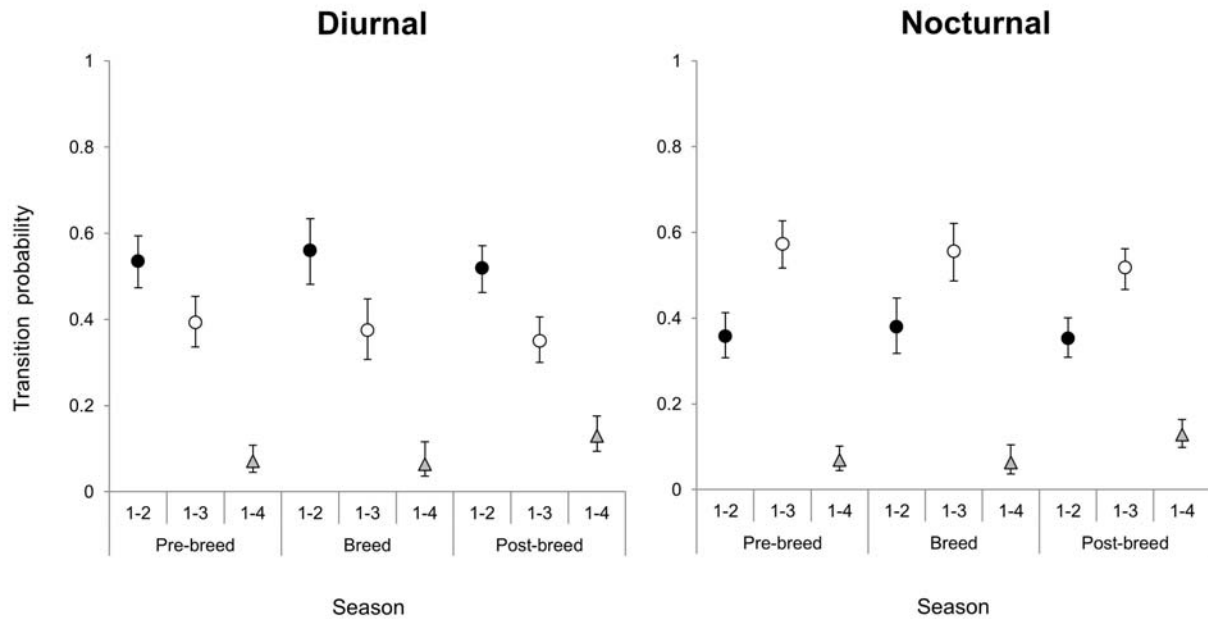
Figure 2. Probability for a feeding site to transition from state 1 – state 2 (solid circle), state 1 – state 3 (hollow circle), and state 1– state 4 (triangle) during diurnal and nocturnal hours. State 1 = no deer present, state 2 = subordinate (adult females and yearling males) present, state 3 = dominant (adult males) present, and state 4 = subordinate and a dominant present. Transition probability for transitions from state 1– state 2 was greater than state 1– state 3 and state 1– state 4 during diurnal hours in all seasons. During nocturnal hours, the transition probability for state 1 – 3 was greater than state 1 – 2 and state 1 – 4 in all seasons.

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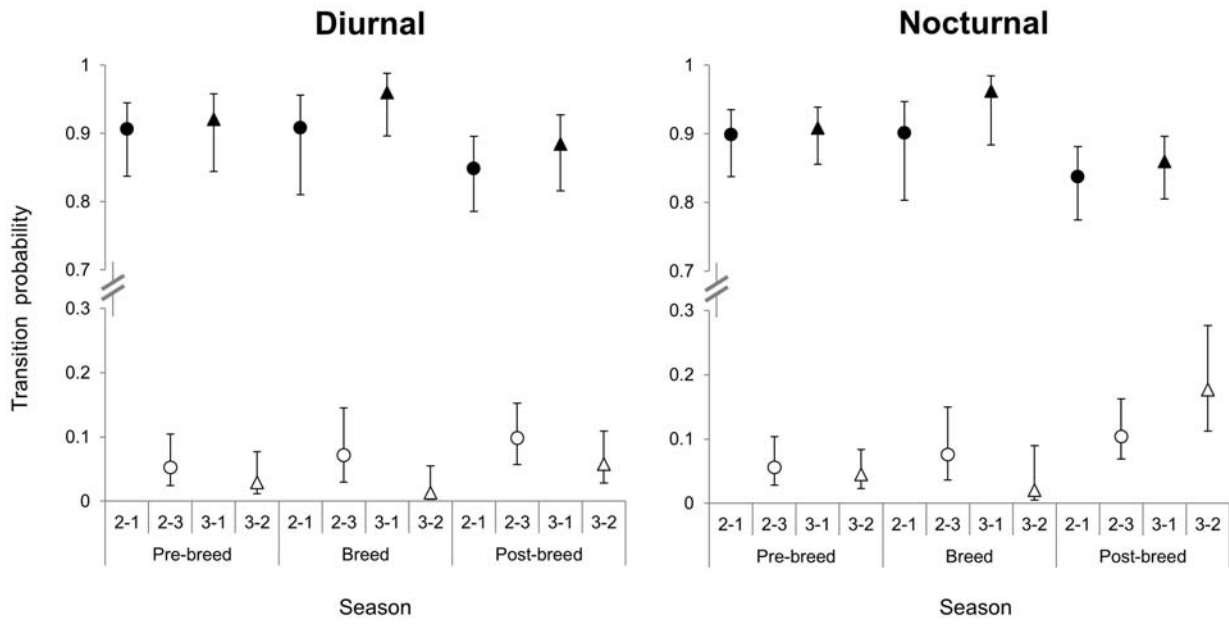
Figure 3 Probability for a feeding site to transition from state 2 – state 1 (solid circle), state 2 – state 3 (hollow circle), state 3– state 1 (solid triangle), and state 3 – state 2 (hollow triangle) during diurnal and nocturnal hours. State 1 = no deer present, state 2 = subordinate (adult females and yearling males) present, state 3 = dominant (adult males) present, and state 4 = subordinate and a dominant present. Transition probability for transitions from state 2– state 1 was greater than state 2 – state 3 during diurnal and nocturnal hours in all seasons. Transition probability for transitions from state 3– state 1 was greater than state 3 – state 2 during diurnal and nocturnal hours in all seasons.
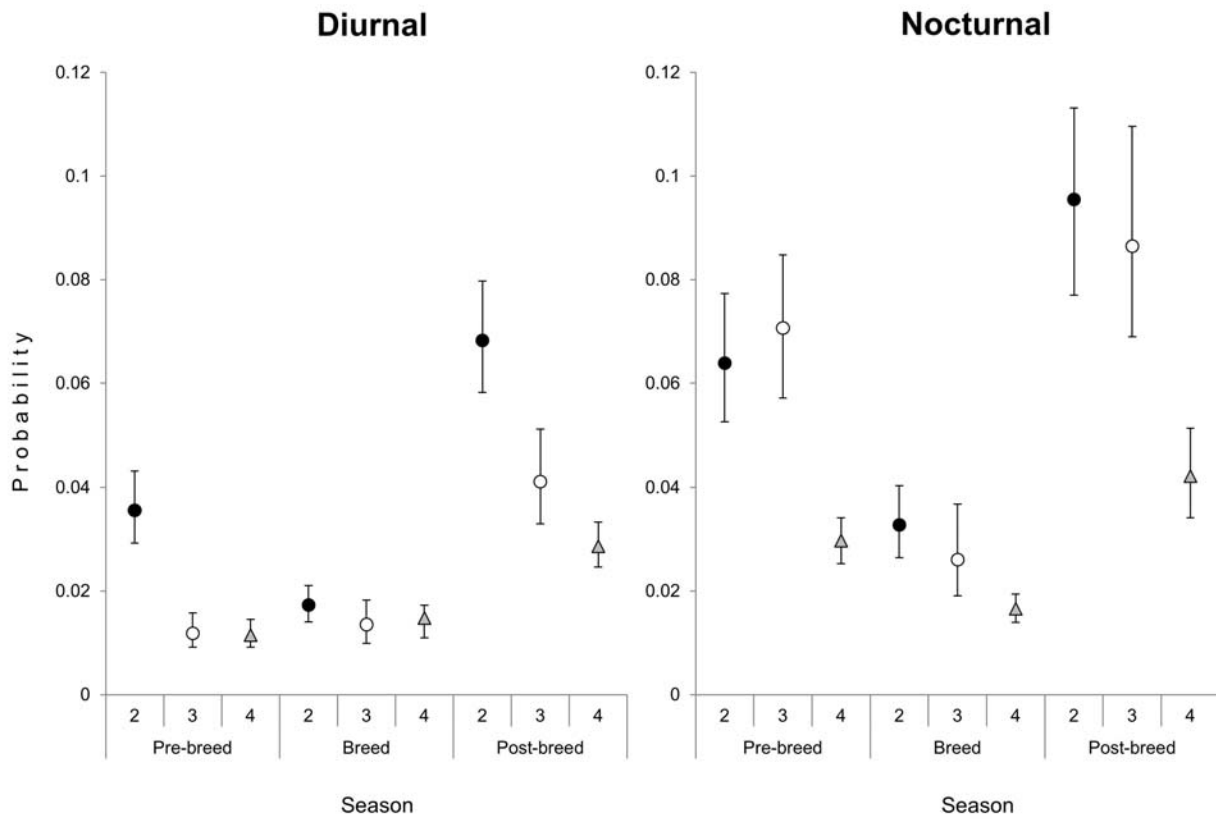
Figure 4. Probability that a feeding site was in state 2 (subordinate present), state 3 (dominant present), or state 4 (subordinate and dominant present) during diurnal and nocturnal hours in the pre-breeding, breeding, and post-breeding seasons. During the pre- and post-breeding seasons, subordinates were more likely than dominants to be at a feeding site during diurnal hours. During all seasons, dominants and subordinates were equally likely to be at a feeding site during nocturnal hours.