

## Parasitism and grooming behavior of a natural white-tailed deer population in Alabama

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We assessed responses in grooming behavior to ectoparasite densities in naturally occurring white-tailed deer (*Odocoileus virginianus*) in southwest Alabama, and tested predictions of the stimulus-driven and programmed grooming models with respect to intraspecific body size and vigilance. Stimulus-driven grooming predicts greater tick densities would lead to an increase in grooming, whereas the programmed model predicts a higher rate of grooming would decrease tick densities. Within the programmed model, smaller individuals are predicted to groom more and host fewer ticks, and, due to increased vigilance, breeding males will groom less than females and bachelor males, and thus host more ticks during the rut. We used generalized linear models to determine males had a higher average tick density than females and exhibited complete separation of tick parasitism between non-rutting and rutting periods. Our results support the stimulus-driven grooming model as both fawns and yearlings had significantly higher deer ked and combined deer ked/tick densities than adults. We used Mann–Whitney U tests to conclude fawns oral groomed at a significantly higher rate than adults, even in the absence of allogrooming. Programmed and stimulus-driven grooming were not mutually exclusive, but rather ectoparasite and host dependent. Although individuals observed grooming were analyzed separately from harvested individuals, we infer that heavy deer ked densities may lead to higher grooming rates. We suggest white-tailed deer grooming for ticks should be considered within an evolutionary framework, and grooming for deer keds should be viewed as a proximate response to agitation. This is the first study to show that deer keds may have a greater influence in overall grooming behavior of deer than do ticks. We recommend that future studies should consider other ectoparasites along with ticks to understand their effects on grooming behavior in dimorphic terrestrial mammals.

KEY WORDS: Alabama, ectoparasites, generalized linear models, grooming, Hippoboscidae, Ixodidae, white-tailed deer.

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## INTRODUCTION

Ectoparasites have an adverse effect on their host and can be considered stressors. Hard ticks (*Ixodida Ixodidae*) are ubiquitous parasites of deer and other cervids that can cause pelage loss, weight loss, anemia and behavioral problems (Durden et al. 1991), and transmit pathogens (Campbell & VerCauteren 2011). Due to their potentially high local abundance, deer keds (*Diptera Hippoboscidae*) are also considered important deer ectoparasites (Demarais et al. 1987), and the ked *Lipoptena mazamae* is as a potential vector of *Bartonella* bacteria that infect vertebrate erythrocytes (Allan 2001; Reeves et al. 2006). Given the impact of both these ectoparasites on deer (ranging from pelage loss to disease), reduction in stressor inputs should be beneficial at the individual and population levels (see Demarais et al. 1987).

Parasite defense grooming is an adaptive behavior because it reduces ectoparasite densities. This type of grooming is regulated by a central control mechanism via hormonal modulation (Meisenberg 1988) and cutaneous stimulation (Riek 1962, in Mooring et al. 2000), and can be explained by programmed and stimulus-driven grooming models. Programmed grooming is controlled by an ultradian clock of the central nervous system, occurs in the absence of any bite stimulus and is influenced by host body size and vigilance (Hart et al. 1992; Mooring & Hart 1995). Smaller (younger) individuals have a comparatively greater surface-area-to-mass ratio than larger individuals, thus sustaining a higher cost of infestation (e.g., blood loss, disease; Hart et al. 1992; Mooring et al. 2000). Therefore, smaller individuals are predicted to groom more than larger individuals in order to prevent attachment of ectoparasites, and hence will host fewer ectoparasites (developmentally dimorphic grooming). During the breeding season, males of polygynous species such as deer show intensified vigilance. This implies a change in time budgets due to increased awareness of rival males and oestrous females. As demonstrated in domestic goats (Mooring et al. 1998; Kakuma et al. 2003), reduced grooming during the breeding season can be attributed to physiological suppression due to high testosterone levels. If increased vigilance impacts grooming behavior, breeding polygynous males are predicted to groom less than both females and bachelor males during a reproductive season (sexually dimorphic grooming), and to host a larger number of ectoparasites. In contrast, stimulus-driven grooming suggests parasitic irritation causes grooming and predicts that those individuals with a greater number of ectoparasites groom more (Hart et al. 1992; Mooring & Samuel 1998). Although programmed and stimulus-driven grooming are not mutually exclusive, depending on the context, one model may explain grooming activity more than the other (Hawlena et al. 2008). Nonetheless, both models imply that an optimal grooming rate balances the cost of ectoparasite infestation against the costs of grooming (Mooring et al. 2002). As grooming behavior is integral to the life history of deer, it is likely that grooming is influenced by the rate of infestation and the identity of local ectoparasites.

The aims of this study were to: (1) characterize the identity and abundance of ectoparasites on white-tailed deer (*Odocoileus virginianus*) in a natural population in southern Alabama; and (2) test the predictions of programmed and stimulus-driven grooming models in this population. If the programmed model largely explains grooming behavior, juveniles (fawns and yearlings) should host fewer ectoparasites than adults due to prophylactic grooming. In addition, during the breeding season (rut), vigilant males should show lower grooming rates and have more ectoparasites than females. However, if the stimulus-driven model explains grooming behavior,

individuals with higher ectoparasite densities should groom at a higher rate than those with lower densities. Accordingly, this study assesses these predictions based on densities of ticks and deer keds in a wild white-tailed deer population.

## METHODS

### *Study site*

This study was conducted in Clarke and Wilcox counties, Alabama, USA, from September 2013 to January 2014 and September 2014 to February 2015. The reproductive season (rut) occurred between January and February in the focal population. The site was owned by Soterra LLC and leased by Hardwood Hunting Club, and encompassed 5.43 km<sup>2</sup> of predominantly deciduous bottomland hardwoods and evergreen forest. Less common habitat included mixed forest, shrub land, grassland, pasture, wooded wetlands and open roadway. Thirteen food plots ranging from 320 to 9300 m<sup>2</sup> were planted in April and September for the spring and winter, respectively, to supplement population nutrition (lablab, cowpeas, milo, rape, crimson clover, chicory, wheat, oat and rye). Anthropogenic activity was minimal, but commercial logging occurred occasionally.

### *Ectoparasites*

The most common ticks in Alabama are the blacklegged deer tick (*Ixodes scapularis*), winter tick (*Dermacentor albipictus*) and lone star tick (*Amblyomma americanum*) (Durden et al. 1991). Adult *I. scapularis* are found in highest densities during the winter (more than any other tick), but their immatures are not common on white-tailed deer. *Dermacentor albipictus* parasitizes deer mostly during the fall, winter and spring (Bishopp & Trembley 1945), and *A. americanum* is primarily a summer tick (Durden et al. 1991). Most ticks parasitize their hosts for hours or days, but the non-host phases of their life cycle are relatively long (McCoy et al. 2013).

Hippoboscid flies are obligate hematophagous ectoparasites of homeothermic vertebrates. The deer ked *Lipoptena mazamae* ranges from South Carolina to Texas and is the only known hippoboscid associated with white-tailed deer in the southeastern United States (Kern 2003). Adult deer keds drop their wings upon finding a suitable host and become permanently associated with an individual (Kern 2003). Unlike ticks, keds do not attach to the host, but move across the skin occasionally biting to take a blood meal.

### *Quantifying ectoparasite density*

We quantified ectoparasite density by examining males and females harvested during the 2013 (15 October–31 January) and 2014 (25 October–10 February) hunting seasons. As ectoparasite counts were obtained from deer harvested by third-party hunters, sample sizes for sexes and cohorts were unpredictable. Using a Petco two-sided flea comb, each harvested individual was examined from the ventral midline to the left lateral surface and from the chest to the anus only where white hair was present (Demarais et al. 1987). All ectoparasites were sampled, stored in 75% alcohol and identified morphologically (Needham 2011). Since there was no reason to suspect the left or right side of an individual hosted more ectoparasites than the other, we doubled abundances to approximate total ectoparasite density present on the ventral surface of each deer. Quantifying ventral ectoparasite densities provided a consistent representation of ectoparasites needed for analyses. Sex, age, mass and harvest date were recorded for each deer.

*White-tailed deer*

White-tailed deer not only exhibit sexual dimorphism but are also developmentally dimorphic. Male and female biological roles are reflected in their morphology, males being generally larger than females. Fawns, upon birth, weigh upwards of 4.1 kg (Verme 1989), yearling males 30 to 50 kg, and mature males 60 to 180 kg (Ditchkoff 2011). The majority of body mass is gained by 2.5 years of age (Leberg & Smith 1993) and begins to level off in subsequent age classes. Fawns (0.5 years) occasionally develop antler “buttons” several months after losing their spotted pelage, approximately 4 months after birth (Ditchkoff 2011). As they age, individuals undergo morphological changes including snout shape and torso size (both shorter in younger deer), posture and musculature (Meares 2001), in addition to antler growth in males. We used these characteristics to sex and age individuals that were observed grooming in the field.

The age of harvested individuals used to quantify ectoparasite density was estimated according to tooth wear and replacement (Cain & Wallace 2003). Individuals were aged in half-year increments assuming conception in January and a 7-month gestation period (Haugen 1959). As recommended by Gee et al. (2002), three cohorts were established: fawns, yearlings and adults. We determined mass using a Cabela’s Big Buck Scale before individuals were field dressed. The small sample size of harvested fawns was due to management practices at the study site to ensure high recruitment of fawns and young males to produce desirable mature males (Jacobson et al. 2011).

*Quantifying grooming behavior*

Field observations of free-ranging individuals were challenging due to the wariness of deer. Behavioral observations were conducted from September 2013–February 2014 and September 2014–February 2015 on food plots using box stands (enclosed hunting platforms). Observations were made for a total of 150 hr with Nikon Action 7 × 35 mm binoculars, and all deer were assumed to be different individuals. The selection of food plots where observations were conducted was randomized to minimize pseudoreplication. Continuous recording and behavior sampling (Martin & Bateson 2007) were implemented to document grooming behavior on multiple individuals. A maximum of four individuals were observed concurrently.

We recorded oral grooming (licking and gnawing) and scratch grooming in fawns, females and males of all ages, including autogrooming and allogrooming. Grooming bouts lasting less than 5 sec were recorded as rates (events · min<sup>-1</sup>), whereas bouts lasting longer than 5 sec were combined as total durations (min · min<sup>-1</sup>) and expressed as proportions (Martin & Bateson 2007). Bouts less than 5 sec were defined as events since individual episodes were difficult to quantify at far distances. Although this was not quantified, it is likely that time spent grooming is positively correlated with parasite removal. Therefore, individuals that invest less time grooming per bout might be less likely to reduce their parasite loads than those that spend more time grooming (e.g., rates vs durations). Observed individuals were aged in half-year increments based upon the morphological features noted above.

*Analytical design*

All statistical analyses were performed using R version 3.0.1 (R Core Team 2013). As the response variables were discrete (count data), variation in ectoparasite density was modeled using generalized linear models (GLM) with a negative binomial error distribution and logarithmic link function. We used a negative binomial distribution due to overdispersion when models were fitted with a Poisson distribution (Ruiz-Fons et al. 2013). Predictors included mass, cohort, sex and rut. Individuals harvested during January and February were recorded as being in rut based upon first observations of fawns and the diffusion of bachelor groups. Mass was coded as a numeric predictor, whereas cohort, sex and rut were coded as factors. Fully saturated models were reduced

to the most parsimonious form in a backwards, stepwise manner using the step function based upon Akaike Information Criteria (AIC; Akaike 1974). Variance Inflation Factor analysis (VIF) was used to detect multicollinearity among model predictors (Zuur et al. 2010). All predictors that yielded a VIF value > 10 were subsequently removed from the model in a backwards, stepwise manner. Final models were validated using the Pearson  $\chi^2$  Goodness of Fit test. Lastly, model residuals were extracted using the resid function and tested for normality using the Shapiro-Wilk test. Grooming behavior was analyzed independently of ectoparasite densities.

Variation in grooming rates and total durations were analyzed using a non-parametric approach due to skewed data with many zeros. A single yearling was observed during the study and was not included in our analyses. We used the Mann-Whitney U test to compare mean values of independent samples (Mooring et al. 2006).

The MASS library was used for modeling (Venables & Ripley 2002) and the car package for VIF analyses (Fox & Weisber 2011). The ggplot2 package (Wickham 2009) was used for graphical development.

## RESULTS

### *Variation in ectoparasite density*

Average values and standard deviations of ectoparasite density per cohort and sex were calculated for each parasite family and combined as an estimate of total ectoparasite density (Table 1). *Lipoptena mazamae* was the most prevalent ectoparasite of our sample. *Dermacentor albipictus* was the most abundant tick, only found in January, followed by *I. scapularis* in November and January, and *A. americanum* in January and February.

With respect to ticks, the interaction between sex and rut was removed from the final model due to quasi-complete separation. A single female out of rut was infested with ticks ( $N_{\text{female}} = 1/5$ ,  $N_{\text{male}} = 0/3$ ; Fig. 1a), but all individuals in rut were infested with ticks ( $N_{\text{female}} = 2/2$ ,  $N_{\text{male}} = 7/7$ ; Fig. 1b). Males not only exhibited complete separation of tick parasitism at the onset of rutting but, on average, had a higher tick

Table 1.  
Averages and standard deviations of ectoparasites per harvested deer.

Sex	Cohort	n	Ixo	Hip	Total
Female	Fawn	0	NA	NA	NA
	Yearling	2	3.0 ± 4.2	34.0 ± 22.6	37.0 ± 18.4
	Adult	5	3.2 ± 4.6	55.2 ± 32.2	58.4 ± 30.8
Subtotal female		7	3.1 ± 4.1	49.1 ± 29.7	52.3 ± 28.2
Male	Fawn	2	8.0 ± 5.7	46.0 ± 62.2	54.0 ± 56.6
	Yearling	2	0.0 ± 0.0	88.0 ± 87.7	88.0 ± 87.7
	Adult	6	19.0 ± 20.6	35.7 ± 24.0	54.7 ± 34.9
Subtotal male		10	13.0 ± 17.5	48.2 ± 45.4	61.2 ± 45.7
Total		17	8.9 ± 14.3	48.6 ± 38.6	57.5 ± 38.6

NA, not applicable. Average ectoparasite density (ectoparasites/deer) and standard deviation per cohort and sex with respect to ticks (Ixo), deer keds (Hip), and total ectoparasite density (Total).

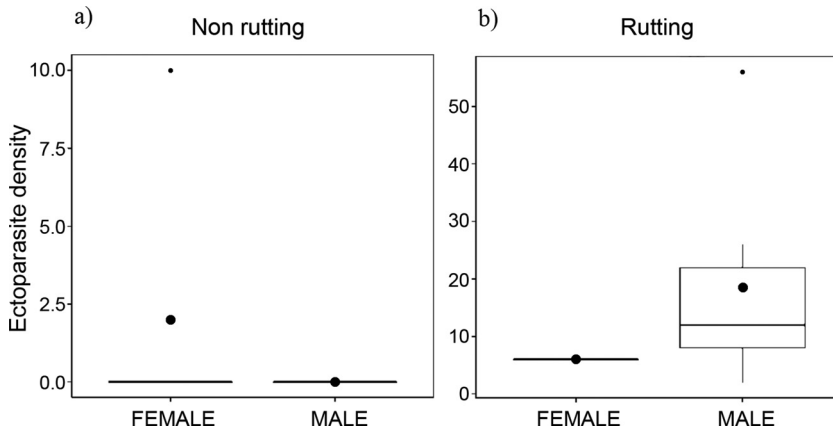


Fig. 1. — Boxplots and mean values (large dots) of interactive effect between sex and rutting activity [(a) non rutting and (b) rutting] on ectoparasite density (ticks/deer).

Table 2.

Statistical results of generalized linear models used to predict variation in discrete data (counts) that is overdispersed.

Predictor	Ixo	Hip	Total
Mass	-	- 0.0569/- 2.719 **	- 0.0517/- 2.558 *
Fawn <sup>a</sup>	-	- 12.4638/- 3.838 ***	- 4.9464/- 2.247 *
Yearling <sup>a</sup>	-	- 5.3032/- 2.477 *	- 5.0875/- 2.452 *
Sex <sup>b</sup>	1.4200/1.647 #	-	-
Rut <sup>c</sup>	-	- 3.3689/- 2.735 **	- 3.8413/- 3.237 **
Mass:Fawn <sup>a</sup>	-	0.4206/4.055 ***	0.1913/2.659 **
Mass:Yearling <sup>a</sup>	-	0.1241/2.420 *	0.1205/2.424 *
Mass:Rut <sup>c</sup>	-	0.0592/2.536 *	0.0720/3.201 **
Intercept	1.1451/1.705 #	6.7977/6.502 ***	6.5604/6.488 ***

<sup>a</sup>In relation to adults.

<sup>b</sup>Males in relation to females.

<sup>c</sup>In rut as related to out of rut.

Coeff./Z and significance level (- not retained, #0.1, \*0.05, \*\*0.01, \*\*\*0.001) of generalized linear models (negative binomial error distribution and logarithmic link function) created to predict ectoparasite density per deer with respect to ticks (Ixo), deer keds (Hip) and total ectoparasite density (Total).

density than females (Table 1). After removing the partial separation from the model, variation in tick density was explained most parsimoniously by sex; males had significantly more ticks than females (Table 2). Mass, cohort and rut were not significant predictors of tick density.

The interactions between mass and cohort, as well as mass and rut, best explained variation in deer ked density. Hippoboscid density decreased significantly with age (per

cohort) for every one unit increase in mass. Males and females in rut had more deer keds per unit increase in mass than individuals out of rut (Table 2). The predictors mass, cohort and rut were therefore retained in the final model, allowing significant interactions with covariates to be considered. Sex was not a significant predictor of deer ked density.

Total ectoparasite density showed a similar pattern to that found for deer keds alone. When combined, tick and deer ked density decreased significantly per cohort as mass increased. With respect to mass, total ectoparasite density was higher on males and females in rut than out of rut (Table 2). Single predictors were significant and retained in the final model. Sex was not a significant predictor of total ectoparasite density.

### *Variation in grooming behavior*

Due to the cautious demeanor of deer, individual observations account for approximately one tenth of the time spent in the field (16 of the 150 hr of field work). In addition to few individual sightings, grooming is also a low-frequency behavior (Li et al. 2014). Averages and standard deviations per cohort and sex were quantified for each type of grooming behavior (Table 3). Not all observed fawns could be sexed during this study.

Grooming rates (bouts < 5 sec) were analyzed separately from durations (bouts > 5 sec). Combined oral auto and allogrooming rates were significantly greater in fawns than adults (Table 4; Fig. 2a), as was the case for oral autogrooming alone (Table 4; Fig. 2b). Combined oral grooming rates did not differ between females and males (Table 4), nor did oral autogrooming alone (Table 4). Finally, when sexes were pooled, combined oral rates did not differ between rutting and non-rutting periods, nor did oral

Table 3.  
Averages and standard deviations of grooming rates and total durations.

Sex	Cohort	n	OR	SR	OD
Female	Fawn	0	NA	NA	NA
	Yearling	0	NA	NA	NA
	Adult	15	0.0100 ± 0.0236	0.0041 ± 0.0096	0.0010 ± 0.0032
Subtotal female		15	0.0100 ± 0.0236	0.0041 ± 0.0096	0.0010 ± 0.0032
Male	Fawn	2	0.0423 ± 0.0598	0	0
	Yearling	1	0	0	0
	Adult	4	0.0211 ± 0.0423	0	0
Subtotal male		7	0.0241 ± 0.0412	0	0
	Fawn <sup>a</sup>	14	0.0426 ± 0.0446	0.0159 ± 0.0279	0.0018 ± 0.0031
Total		36	0.0254 ± 0.0384	0.0079 ± 0.0192	0.0011 ± 0.0028

<sup>a</sup>Sex not determined.

NA, not applicable. Grooming rates (events · min<sup>-1</sup>) and total durations (min · min<sup>-1</sup>) of combined autogrooming and allogrooming (OR, oral rate; SR, scratch rate; OD, oral duration) per cohort and sex.

Table 4.  
Statistical results of Mann-Whitney U tests.

Comparison		W	N	N	P
Rates – oral grooming					
Fawns vs adults	Auto + allogrooming	90	$N_{\text{fawns}} = 16$	$N_{\text{adults}} = 19$	<b>&lt; 0.05</b>
	Autogrooming	218	$N_{\text{fawns}} = 16$	$N_{\text{adults}} = 19$	<b>&lt; 0.05</b>
Females vs males	Auto + allogrooming	50	$N_{\text{females}} = 15$	$N_{\text{males}} = 6$	0.6604
	Autogrooming	38	$N_{\text{females}} = 15$	$N_{\text{males}} = 6$	0.4981
Rut vs non-rut	Auto + allogrooming	90	$N_{\text{rut}} = 8$	$N_{\text{non-rut}} = 27$	0.4459
	Autogrooming	93	$N_{\text{rut}} = 8$	$N_{\text{non-rut}} = 27$	0.52
Rates – scratch grooming					
Fawns vs adults		181	$N_{\text{fawns}} = 16$	$N_{\text{adults}} = 19$	0.1995
Durations – oral grooming					
Fawns vs adults	Auto + allogrooming	174	$N_{\text{fawns}} = 16$	$N_{\text{adults}} = 19$	0.2784
	Autogrooming	164	$N_{\text{fawns}} = 16$	$N_{\text{adults}} = 19$	0.5138

Comparison of oral and scratch grooming rates and durations between cohorts and rutting periods. Significant *P*-values are in bold.

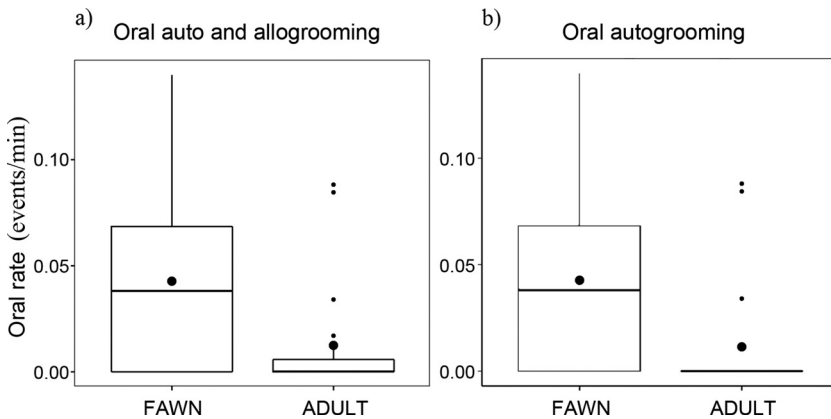


Fig. 2. — Boxplots and mean values (large dots) of total rates of (a) oral grooming and (b) oral autogrooming (allogrooming removed) between fawns and adults.

autogrooming alone (Table 4). Scratch grooming rates did not differ between fawns and adults (Table 4). No males scratch groomed ( $N = 0/6$ ), but some females did ( $N = 3/15$ ). No scratch grooming occurred during the rut ( $N = 0/8$ ) for either sex.

In contrast to grooming rates, combined oral auto and allogrooming durations did not differ between fawns and adults, nor did autogrooming durations alone (Table 4). No males oral groomed in the form of durations ( $N = 0/6$ ), but females did ( $N = 2/15$ ), and no oral grooming durations were observed during the rut ( $N = 0/8$ ) for either sex. No males



oral autogroomed in the form of durations ( $N = 0/6$ ), but females did ( $N = 2/15$ ). No oral autogrooming durations were observed during the rut ( $N = 0/8$ ) for either sex. No scratch grooming durations were observed during this study ( $N = 0/36$ ).

Grooming rates and total durations between sexes during the rut could not be analyzed as only a single adult female that did not groom was observed. One fawn and one adult of five males observed during the rut groomed at an oral rate of  $0.0845 \text{ events} \cdot \text{min}^{-1}$ .

## DISCUSSION

This study examined harvested male and female Alabama white-tailed deer in various age classes to assess the density of tick and deer ked ectoparasites. We then related ectoparasite densities to field observations of grooming behavior to test predictions of two grooming models. The programmed grooming model predicts smaller individuals will groom more than larger ones and are expected to host fewer ectoparasites. Because programmed grooming is modulated by hormones (Meisenberg 1988), vigilant males are expected to groom less and host a greater density of ectoparasites than females and immature males during the rut. In contrast, if grooming is a consequence of cutaneous stimulation, then ectoparasite density should influence grooming rates as predicted by the stimulus-driven model.

We found no support for the programmed grooming prediction that smaller (younger) individuals would have reduced ectoparasite loads of ticks, deer keds or total ectoparasite densities due to prophylactic grooming. Juveniles had significantly higher deer ked and total ectoparasite densities than adults per unit increase in body mass (Tables 1–2). This, combined with higher oral grooming rates in fawns versus adults (Table 4), supported stimulus-driven, responsive grooming. Higher densities of deer keds and total ectoparasites on juveniles compared to adults explain the higher rates of combined oral auto and allogrooming (Fig. 2a) and oral autogrooming alone (Fig. 2b). As there were insufficient observations on yearlings for analysis, the main support for stimulus-driven grooming lies in the differences between fawns and adults. The interaction between mass and age best explains the decrease in total ectoparasite density. Higher densities on younger individuals may be the result of fawns bedding more than adults to avoid predation, or horizontal transmission resulting from allogrooming with siblings and mothers. To establish a direct link between ectoparasite load and grooming, however, the same individual deer would need to be monitored for both, which was not possible in this study. Future studies of wild populations should therefore consider ectoparasites and grooming behavior simultaneously to determine whether grooming results from proximate agitation or an evolved, programmed response.

Overall, males hosted more ticks than females (Tables 1–2), but the interaction between sex and rutting activity was not included in modeling due to quasi-complete separation (Fig. 1; Table 2). This makes it likely that heightened vigilance played a role in the increased tick density on males during the rut, and supports the prediction that vigilance can decrease baseline, programmed grooming for ticks. Although the vigilance principle (Hart et al. 1992) primarily focuses on sex-related parasitism during the rut, it is evident that levels of vigilance change between rutting and non-rutting periods. We note that our observed variation in tick parasitism in and outside the rut should not be attributed to seasonal fluctuations in environmental tick abundance. Grooming rates can be predicted to adjust seasonally as ectoparasite abundance fluctuates temporally (Durden et al. 1991; Mooring et al. 2004).

If male tick densities are predicted to differ from females and immature males during the rut, breeding males are also expected to host more ticks during the rut than outside of it. This reflects temporal changes in vigilance as males begin to exhibit rutting behavior (e.g., chasing, tending, mating, and fighting rivals). During the rut, we found tick densities were higher on males than on females (Fig. 1b). Although post hoc analyses were not performed on the subset of males and females, the separation and higher rate of ectoparasitism on rutting males suggests that increased vigilance reduces baseline, programmed grooming. Here we found partial separation by sex where males were parasitized during the rut but not outside the rut, whereas females were parasitized in and out of rut. Complete separation would occur if rutting activity separated parasitism for both sexes in and out of the rut. In future studies, larger sample sizes would be particularly important if post hoc analyses are deemed necessary due to partial separation of males and females.

We found that white-tailed deer grooming at our study site was predominately stimulus-driven with an underlying rate of programmed grooming. Programmed grooming for ticks should be considered within an evolutionary framework, as selective pressures may have shaped current cervid behaviors during the evolution of artiodactyls (e.g., Mooring et al. 2002). For instance, decreased levels of programmed grooming in rutting males may result from heightened vigilance and physiological suppression by increased testosterone (Bubenik et al. 1990; Mooring et al. 1998; Kakuma et al. 2003; but see Li et al. 2014). Conversely, we hypothesize that stimulus-driven grooming in response to deer keds might be a proximate response to agitation. Ectoparasite biology seems to have an effect on grooming behavior: while ticks attach to the host and bite a single time, deer keds cause a potentially higher level of irritation as they move across the host body and bite multiple times. This study corroborates the assertion that the two grooming models are not mutually exclusive, but ectoparasite and host dependent (Hawlena et al. 2008), thus underscoring the importance of examining multiple species of ectoparasites in wild populations.

This is the first study that includes deer keds and ticks to test programmed and stimulus-driven grooming in exclusively wild white-tailed deer. Although studies on captive dimorphic terrestrial mammals have provided useful information about the evolution of grooming behavior by controlling for stimulus-driven grooming (Mooring et al. 2000, 2002, 2004; Li et al. 2014), they often focus on few individuals, or have short observation periods. A multivariate approach to studying ectoparasitism as it relates to grooming in wild populations therefore remains to be further explored. This can be seen from the groundwork presented here that included 12 months of observations in 2 consecutive years. If expanded to a larger number of white-tailed deer populations that inhabit other areas across North America, such an approach could provide a more comprehensive view into the natural history of deer ectoparasites, and a broader comprehension of the evolution of grooming. We hope this work contributes to our understanding of the behavior and ectoparasitism of North America's most common game species, and that it inspires future behavioral ecology work on wild populations of white-tailed deer.

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## DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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