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RESEARCH ARTICLE

Effects of Immunocontraception on Behavior in Fallow Deer (*Dama dama*)

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Immunocontraceptives can control growth in wild and captive populations; however, in doing so, they should not disrupt species-typical behavior patterns. The presence of treated females could disrupt social interactions in a population; yet, few studies have examined effects of immunocontraception on behavior. The goal of this project was to determine whether behavior in a fallow deer (*Dama dama*) population vaccinated with porcine anti-zona pellucida (pZP)-immunocontraceptives differed from behavior in a population of unvaccinated deer. We predicted that pZP-treated females would spend a higher percentage of time exhibiting mating and dominance behavior than nontreated females, and that males interacting with pZP-treated females would spend a higher percentage of time demonstrating mating and aggressive behavior than males interacting with nontreated females. We recorded activity budgets of males and females in two fallow deer populations, one pZP-treated and the other untreated, before, during, and after rut. Females did not differ in time spent displaying mating or dominance behavior compared to nontreated females. Males coexisting with nontreated females spent more time exhibiting aggressive behavior during rut than males living with pZP-treated females, but males did not differ in time spent in mating behavior. Thus, immunocontraception did not seem to affect behavior adversely. However, sample sizes, living conditions, and sex ratios may have affected the results. Given these limitations, future research is needed to confirm our findings. Zoo Biol 27:49–61, 2008. © 2007 Wiley-Liss, Inc.

Keywords: pZP-immunocontraception; wildlife contraception; social interaction

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INTRODUCTION

As human populations expand, some species, such as gray bats (*Myotis grisescens*) and American bison (*Bison bison*), do not adapt well and experience population declines [Macdonald, 2001]. However, species that adjust well to humans, such as white-tailed deer (*Odocoileus virginianus*), raccoons (*Procyon lotor*), and coyotes (*Canis latrans*), may increase [Miller et al., 2001]. Historically, biologists have managed population sizes using hunting, trapping, and relocation [Gogan et al., 2001], but these practices face increasing ethical criticism [McShea et al., 1997]. A recently developed technique, immunocontraception, may provide a more acceptable approach to population management [Kirkpatrick et al., 1996].

Immunocontraception, a method of population control administered to wild and captive animals, uses an animal's immune system to prevent fertilization [Muller et al., 1997]. Several types of immunocontraceptives exist, but this study focused on behavioral effects of porcine anti-zona pellucida (pZP)-immunocontraceptives, which block or modify sperm receptors located on the egg's zona pellucida [Barber and Fayrer-Hosken, 2000].

To be effective, population control methods should not affect hormones that influence behavior, including social interactions. Most researchers believe that pZP-immunocontraception does not disrupt normal behavior nor does it affect hormone levels, because the vaccine carries no hormones [Delsink et al., 2002]. Yet, even though hormones are not affected directly, the presence of immunocontracepted females that never allocate energy to offspring could disrupt social interactions in a population.

Researchers studying behavioral effects of immunocontraceptives generally found that behavior was affected to some degree. In a small fallow deer (*Dama dama*) herd, a male mounted an immunocontracepted female and ignored fertile females [Fraker et al., 2002]. Immunocontracepted elephants (*Loxodonta africana*) did not show changes in dominance rank or frequency of social behavior patterns; however, some herd movement patterns became unpredictable when animals reacted to the darting process [Delsink et al., 2002]. Elk (*Cervus elaphus*) treated with immunocontraceptives showed no overall change in herd behavior, but treated females continued to copulate at levels observed during the mating season, even 6 weeks after the mating season ended [Heilmann et al., 1998]. However, these studies included a small number of vaccinated females, and observations came only from single populations. In addition, they focused on female behavior patterns and on male–female interactions, but they did not consider behavior among males.

We studied fallow deer to evaluate possible effects of pZP-immunocontraception on mating, dominance, and aggressive behavior, and thus to determine whether the use of immunocontraceptives preserved or disrupted normal behavior patterns. Owing to its adaptability across wide geographic areas, the species occurs in zoos and reserves worldwide [Mattiello et al., 1997]. Under confinement, fallow deer maintain social and mating behavior typical of the species [Mattiello et al., 1997], and immunocontraceptives have proven effective [Deigert et al., 2003].

We predicted that pZP-treated females would spend more time exhibiting mating behavior than nontreated females because pZP-treated females do not become pregnant and thus may continue their estrous cycles throughout the breeding season [Fraker et al., 2002]. We also predicted that pZP-treated females would spend more time displaying dominance behavior than nontreated females because general activity levels increase during estrus [McShea et al., 1997]. We predicted that males interacting with pZP-treated females would spend more time demonstrating mating behavior compared to males interacting with nontreated females because the former would continue to breed females in estrus. Finally, we predicted that males interacting with pZP-treated females would spend more time showing aggressive behavior because they would compete for access to estrous females [McElligott and Hayden, 2000].

METHODS AND MATERIALS

Study Populations

We identified two study populations. The first population, housed at York's Wild Kingdom, is located in southern Maine (43.10°N, 70.37°W). This zoo houses up to 60 fallow deer year round, and about 55% are females. Deer are kept in one of three outdoor pens at any time. During the day, deer have access to a 46 × 24 m front pen with sand substrate and trees. At night, animals are herded into a 24 × 31 m back pen with loam substrate and two shelters. A third pen is used to separate animals if necessary. Each pen holds its own hay feeder. The population is fed a diet of hay and grain as well as any grass they obtain in the pens. We identified individuals using unique coat colors and markings. No deer were vaccinated with immunocontraceptives. In September 2005, zoo staff reduced the number of males from 15 to seven to guard against injury, and we observed the remaining 37 individuals.

The second population resides in Cooperstown, NY (42.70°N, 74.90°W). This population is supervised by the Clark Foundation and consists of up to 65 animals, with about 92% females. At the start of this study, the herd consisted of 52 females and five males. The population is kept in an outdoor 700 × 700 m pasture and fed a diet of grain and hay as well as grass from the pasture. We identified each animal by a colored ear tag or by unique markings. In 1998, 21% of females initially received pZP-immunocontraceptives, followed by 83 and 97% in 1999 and 2000, respectively [Deigert et al., 2003]. By 2001, all females were vaccinated [Deigert et al., 2003], and they received annual boosters through fall 2004. In fall 2004, all females except nine received boosters.

Observations were blind to females' contraceptive status in the Cooperstown herd. Herd managers identified pZP-treated individuals using tattoo numbers that we could not see from a distance. In February 2006, the herd was tested for tuberculosis and reimmunocontracepted. At that time, we identified females that did not receive boosters in the previous year.

Data Collection

The senior author and a field assistant observed deer from July to December 2005. Rut typically occurred for 3 weeks in late October and early November in both populations; therefore, we obtained data before, during, and after the breeding season. We collected a total of 62 hr of focal observations in both herds (27 focal hours in Cooperstown and 35 focal hours at York's Wild Kingdom) collected over 52 days (25 days in Cooperstown and 27 days at York's Wild Kingdom). Observers always worked together to collect data in each population. We practiced observation techniques in June to consistently record data, and we simultaneously observed animals as we stood together during every observation period, further ensuring that we were consistent in our techniques. We collected data twice daily, weather permitting, and each observation period lasted 0.5–3 hr. The length of observation periods did not differ across the study. We began at sunrise and continued until the herd reclined for the day. We observed again in the afternoon/evening when at least 10 individuals were standing, and we continued until dark. The number of morning and afternoon/evening sessions was nearly equal for Cooperstown (62 and 67, respectively), whereas we collected slightly more data during the afternoon/evening at York's Wild Kingdom (84 morning and 103 afternoon/evening observations).

In Cooperstown, we observed deer from outside the pen along the fence, where deer were less likely to notice us owing to the steady flow of pedestrians, and we used spotting scopes because we were positioned at least 400 m from the animals. In York, we observed outside the gate, where we could see the majority of the pen. Owing to the smaller size of the pen, we did not use spotting scopes.

We randomly chose individuals to observe. However, we did not observe every animal, and we sampled some individuals multiple times. The order in which we observed animals was not biased in either observation period. We observed each individual continuously for 15 min, and each animal was observed only once per day. If an individual moved out of view or reclined while we observed it, we waited up to 2 min. If the focal animal did not return or stand up within that time, we stopped the observation and chose a new focal animal. We recorded duration of each behavior pattern onto an audio recorder and transcribed tapes later that day.

We used an ethogram compiled from several sources to direct our data collection (Table 1). We followed other authors' classifications and assigned "approach" as a dominant or aggressive behavior pattern because animals often initiated aggression or dominance interactions by first moving toward another individual or a subordinate [Kitchen, 1974; Maher and Byers, 1987].

Data Analysis

We originally collected data in units of time. As we did not observe each focal individual for a full 15 min, we converted raw data into percentages. We summed individual variables to create three composite variables: mating behavior, dominance behavior, and aggressive behavior (Table 1). We also defined periods of time in relation to mating season (rut) status. Prerut included data gathered from July to September (13 focal hours in Cooperstown; 13 focal hours in York). Rut included data gathered from October to November (12 focal hours in Cooperstown; 19 focal hours in York), and postrut included data collected in December (2.5 focal hours in Cooperstown; 3 focal hours in York).

We calculated a mean for each individual for each category and time period and used these means in our analyses. Using JMP [SAS Institute Inc., 2004], we carried out nonparametric Mann–Whitney *U*-tests to compare behavior between herds because data were not normally distributed and sample sizes were small in some cases. We also used post hoc power analysis on results that were not statistically significant ($P \geq 0.05$) to detect the probability of making a type II error.

TABLE 1. Fallow deer social behavior categories and descriptions[a]

Category and behavior pattern	Description
Mating behavior patterns in males and females	
Lick	Individual running its tongue on another deer's body
Smell urine	Breathing in the scent of a female's fluid waste
Herd	Rounding up and causing group of females to move
Point tongue	Male sticking out his tongue repeatedly
Rest chin	Male placing his chin on a female's body
Head rub	Male moving his head against a female
Mount	Male attempting or succeeding at copulation
Flehmen	Male raising upper lip toward female
Sniff	Individual breathing in the scent of another
Groom	Individual cleaning another using teeth, lips, and tongue
Guard female	Male preventing another male from approaching a female(s)
Nudge female	Male pushing a female with his head
Dominance behavior patterns in females	
Displace	Individual moving an individual from its original location
Approach	Individual walking toward another individual
Bite	Individual pinching another individual's skin between its teeth
Head lower	Individual lowering its head in the direction of another deer
Aggressive behavior patterns in males	
Displace	Individual moving an individual from its original location
Chase	Male following an individual quickly for >5 steps
Bite	Individual pinching another individual's skin between its teeth
Contact	Antlers touching and pushing against another male's antlers
Head lower	Individual putting its head down in the direction of another
Approach	Individual walking toward another individual

[a]Ethogram definitions were compiled from previous studies [Bartos, 1982; Braza et al., 1986; Heilmann et al., 1998].

RESULTS

Fallow deer did not differ in the percentage of time spent in aggression or dominance activity between morning and afternoon/evening sessions ($P > 0.23$, power < 0.184), and deer in York did not differ in mating behavior between sampling sessions ($P = 0.83$, power $= 0.37$). In Cooperstown, females during rut engaged in more mating activity in the morning versus the afternoon/evening sessions (morning: $3.8 \pm 1.6\%$, $n = 23$; afternoon/evening: $0.26 \pm 0.19\%$, $n = 19$; $z = -2.82$, $P = 0.005$). Cooperstown males, however, did not vary their activity patterns depending on time of day ($P = 0.40$, power $= 0.05$). Because results were not consistent across populations or sexes, and because most variables did not differ by time of day, we pooled samples across the day.

Over the entire season, pZP-treated Cooperstown females did not differ in the percentage of time spent exhibiting mating behavior compared to York females ($P = 0.12$, power $= 0.21$; Table 2). The percentage of time spent demonstrating mating behavior between these two groups also did not differ in any time period

TABLE 2. Mean (±SE) percentage of time that fallow deer spent exhibiting behavior patterns over the entire study period, July–December 2005

Population	Mating behavior	Dominance behavior	Aggressive behavior
York			
Females (19)	0.20±0.20	0.20±0.10	
Males (15)	1.70±1.60		3.70±1.60
Cooperstown			
pZP-treated females (24)	0.02±0.02	0.60±0.50	
Nontreated females (9)	0.10±0.10	1.70±1.40	
Males (5)	1.20±0.80		0.10±0.10

Sample sizes are indicated in parentheses.

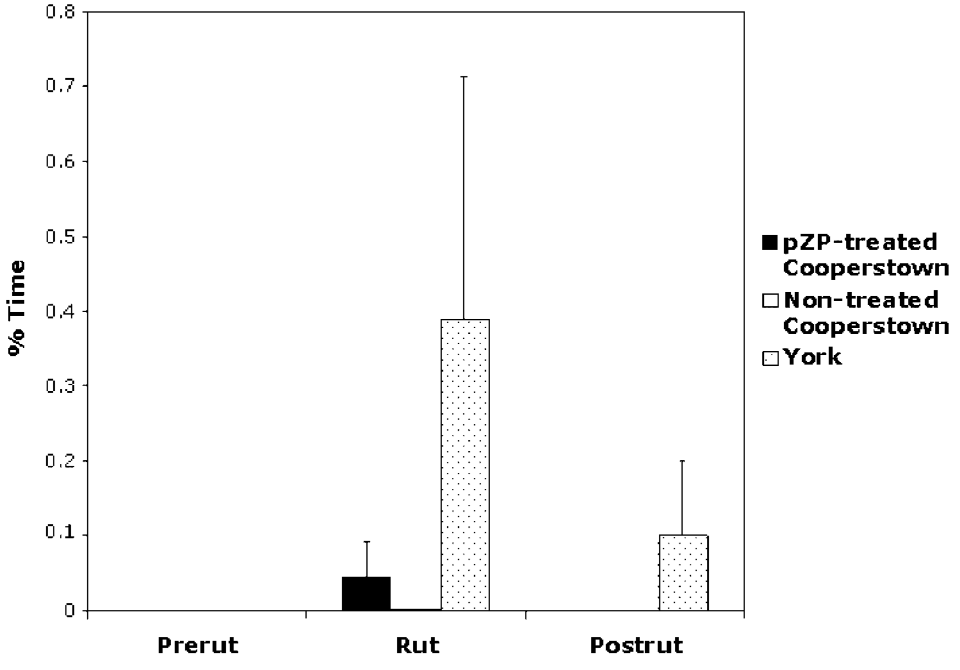

Fig. 1. Percentage of time (+SE) that porcine anti-zona pellucida-treated and nontreated fallow deer females spent exhibiting mating behavior in Cooperstown, NY, and York, ME. Sample sizes: prerut: $n = 15$, 7, and 18 females; rut: $n = 14$, 7, and 16 females; postrut: $n = 6$, 2, and 7 females. For definitions of behaviors included in the mating category, see Table 1.

(prerut: $P = 1.00$; rut: $P = 0.22$, power = 0.16; postrut: $P = 0.35$, power = 0.13; Fig. 1). Furthermore, nontreated Cooperstown females did not differ from York females over the entire season in the percentage of time spent displaying mating behavior ($P = 0.97$, power = 0.31; Table 2), and these two groups did not differ during prerut, rut, or postrut (prerut: $P = 1.00$; rut: $P = 0.93$, power = 0.08; postrut: $P = 0.59$, power = 0.07; Fig. 1).

From July to December, pZP-treated Cooperstown females did not differ from York females in the percentage of time spent on dominance behavior ($P = 0.96$,

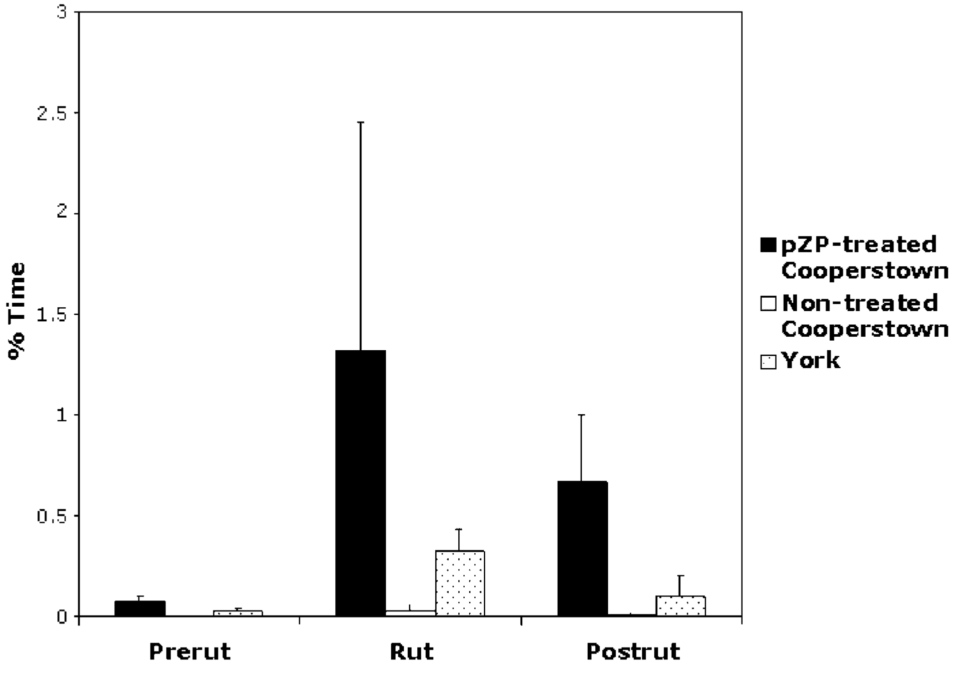

Fig. 2. Percentage of time (+SE) that porcine anti-zona pellucida-treated and nontreated fallow deer females spent exhibiting dominance behavior in Cooperstown, NY, and York, ME. Sample sizes: prerut: $n = 15$, 7, and 18 females; rut: $n = 14$, 7, and 16 females; postrut: $n = 6$, 2, and 7 females. For definitions of behaviors included in the dominance category, see Table 1.

power = 0.16; Table 2), and these two groups did not differ in time spent exhibiting dominance behavior over time (prerut: $P = 0.40$, power = 0.25; rut: $P = 0.18$, power = 0.15; postrut: $P = 0.16$, power = 0.29; Fig. 2). In addition, throughout the season, nontreated Cooperstown females did not differ from York females in the percentage of time spent demonstrating dominance behavior ($P = 0.49$, power = 0.34; Table 2). The two groups did not differ over time (prerut: $P = 0.44$, power = 0.13; rut: $P = 0.77$, power = 0.31; postrut: $P = 0.23$, power = 0.23; Fig. 2).

Cooperstown males did not differ in the percentage of time spent exhibiting mating behavior compared to York males over the entire season ($P = 0.48$, power = 0.05; Table 2). Furthermore, the percentage of time spent displaying mating behavior did not differ between herds during prerut, rut, and postrut (prerut: $P = 0.45$, power = 0.30; rut: $P = 0.66$, power = 0.06; postrut: $P = 0.11$, power = 0.34; Fig. 3).

Over the entire season, Cooperstown males did not differ in the percentage of time spent exhibiting aggressive behavior compared to York males ($P = 0.08$, power = 0.26; Table 2). However, during rut, York males spent a significantly higher percentage of time displaying aggressive behavior compared to Cooperstown males ($\chi^2 = 7.16$, $n = 7$ and 4, $P = 0.01$; Fig. 4), whereas they did not differ during prerut or postrut (prerut: $P = 0.23$, power = 0.15; postrut: $P = 1.00$; Fig. 4).

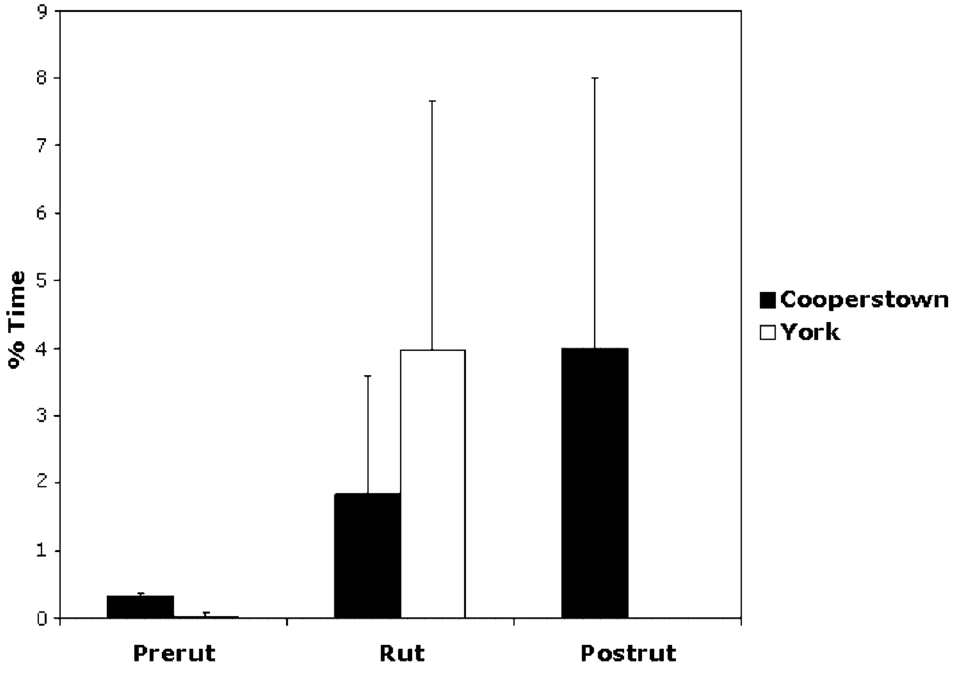

Fig. 3. Percentage of time (+SE) that fallow deer males spent exhibiting mating behavior in Cooperstown, NY, and York, ME. Sample sizes: prerut: $n = 5$ and 12 males; rut: $n = 4$ and 7 males; postrut: $n = 2$ and 5 males. For definitions of behaviors included in the mating category, see Table 1.

To detect a moderate difference ($d = 0.50$) with power equal to 0.80, we needed a minimum sample size of 27 individuals [Kraemer and Thiemann, 1987]. We sampled sufficient number of females to detect such differences, but the populations contained fewer numbers of males.

DISCUSSION

We did not detect behavioral differences between fallow deer from a pZP-treated herd and a nontreated herd, contradicting previous studies that found differences in behavior of pZP-treated populations [Heilmann et al., 1998; Powell, 1999; Delsink et al., 2002; Fraker et al., 2002]. We expected to see differences in the percentage of time that pZP-treated females spent displaying mating behavior compared to nontreated females, especially after rut. Normally, most females become pregnant during rut, and mating behavior decreases thereafter [Heilmann et al., 1998]. However, as pZP-treated females could not conceive, they probably would continue to cycle [Fraker et al., 2002] and thus prolong the mating season. In contrast, nontreated females tended to spend more time in mating behavior than pZP-treated females, although differences were not statistically significant. Differences in living conditions of the two herds might explain these results. Nontreated females in York resided in a smaller pen than pZP-treated females in Cooperstown. Also, seven males had access to 30 nontreated females in York (sex

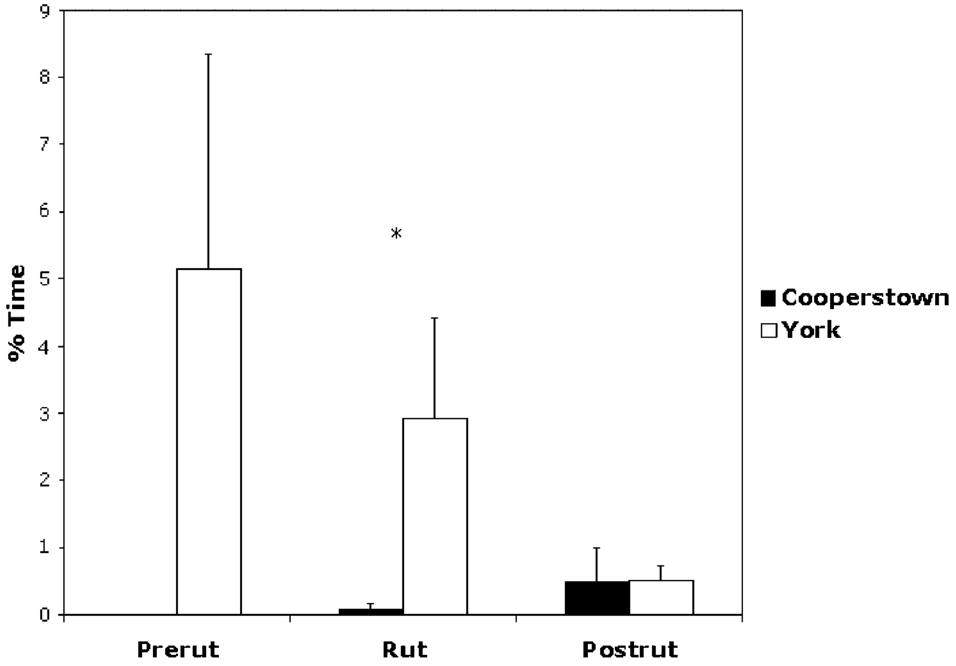

Fig. 4. Percentage of time ($\pm$SE) that fallow deer males spent exhibiting aggressive behavior in Cooperstown, NY, and York, ME. prerut: $n = 5$ and 12 males; rut: $n = 4$ and 7 males; postrut: $n = 2$ and 5 males. For definitions of behaviors included in the aggression category, see Table 1. $^*P < 0.01$.

ratio = 1:4.3), whereas five males resided with 52 pZP-treated and nontreated females in Cooperstown (sex ratio = 1:10.4). Pen size, in combination with sex ratio, provided an opportunity for nontreated York females to encounter males more often and thus exhibit more mating behavior. As the Cooperstown herd contained nine nontreated females, we compared percentage of time that nontreated females in both herds displayed mating behavior and found no difference, which suggests that pen size was not an important factor. However, statistical power was low (<0.31).

Unexpectedly, females from the two populations did not differ in time spent exhibiting dominance behavior. We predicted that nonpregnant pZP-treated females would spend more time in dominance interactions than nontreated females to gain access to males. If so, herd structure might be affected negatively if pZP-treated females spent more time on dominance behavior and restricted subordinate females' access to food or mates. Females living in captivity may not face the same food restrictions as wild females; hence, dominance interactions may play less important roles in captive herds.

As pZP-treated females were not fertile and did not become pregnant, we expected males to continue displaying mating behavior beyond the usual breeding season. Fraker et al. [2002] reported two cases in which a male chose to mate with a pZP-treated female versus nontreated females. However, in this study, males residing with pZP-treated females did not differ in time spent demonstrating mating behavior compared to males residing with nontreated females. As mentioned previously, pen sizes and sex ratios were not equal between populations. Living in a smaller pen, males in the nontreated herd could encounter females more frequently than males in the pZP-treated herd, which may have contributed to the higher amount of time spent on mating behavior during rut.

With pZP-treated females not becoming pregnant, we expected males to spend more time demonstrating aggressive behavior as they sought access to females. Contrary to predictions, during rut, males living with nontreated females in York spent a higher percentage of time displaying aggressive behavior, whereas behavior in prerut and postrut did not differ. Again, restrictions on pen size may have contributed to higher levels of aggressive behavior in York. With individuals living in tighter quarters, they may have contacted each other more often, leading to more interactions. In separate instances during rut in York, two females died when males pinned them against the fence. Furthermore, differences in sex ratios may have increased competition among males in York versus Cooperstown, leading to more aggressive behavior in the former population.

We observed one York male that spent a relatively large proportion of time exhibiting aggressive behavior during one observation period in September (prerut). Later in the year, he did not continue to interact at this high level. Data from this individual account for the high percentage of time spent in aggressive behavior during prerut. Including these data in the analyses increased standard error (0.032 versus 0.017 without his data) and increased the level of aggression in York during prerut compared to rut. Without this one observation, the percentage of time that males with nontreated females spent exhibiting aggressive behavior was higher during rut than prerut, as expected. Several factors may have contributed to this male's spike in aggressive behavior. York's Wild Kingdom was open to the public throughout summer. In September, visitor attendance decreased and the zoo closed. With less pressure from people, deer may be more likely to display natural behavior. Also, in early September, the zoo director removed all males except seven to reduce risk of injury during rut. This culling may have altered herd structure, causing individuals to change their behavior patterns as they sorted out a new hierarchy.

Overall, this study suggests that pZP immunocontraception did not influence mating, dominance, and aggressive behavior patterns in these two fallow deer populations. These data were quite variable, which may have obscured some patterns, but in general, behavioral data are highly variable [Ploger and Yasukawa, 2003]. Nonetheless, several factors may have affected the results, including small sample sizes, skewed sex ratios, and differences in living conditions. Small populations and skewed sex ratios may compound reproductive skew among males. In many ungulates, including fallow deer, a few males may monopolize breeding opportunities [McElligott et al., 1998; Say et al., 2003]. Given the small number of males in our study populations and our random sampling methodology, we probably missed some mating activity, such as copulations, because we were more likely to sample females. We only observed one male copulating during the study, although this low number is supported by other studies in which observers witnessed just 21–33% of males mating [Say et al., 2003]. Furthermore, fallow deer, like other ungulates, are active at night [Kitchen, 1974; Chapman and Chapman, 1975; Borkowski and Pudelko, 2007]. We did not observe animals after dark; hence, we may have missed some mating activity at that time.

Another potential factor influencing these results was prolonged immunocontraception with pZP. Some females in the Cooperstown population had been vaccinated since 1998, and long-term treatment may or may not have long-term effects on reproductive function [Stoops et al., 2006; Patton et al., 2007]. Some studies reported no adverse histologic or physiologic effects [McShea et al., 1997], whereas other studies described ovarian pathologies, some of which negatively affected fertility [Stoops et al. 2006; Curtis et al. 2007]. Domestic sheep (*Ovis aries*) were affected most dramatically compared to other species, with some females experiencing infertility after immunocontraception; however, greater similarity between sheep and pig epitopes may have contributed to the response in this species compared to wild species [Stoops et al., 2006].

In addition, the number of observations varied across the two herds. We performed more observations in York's Wild Kingdom (187) than in Cooperstown (129). As York's Wild Kingdom's pen was smaller, we could locate individual animals more easily. Also, the observers lived closer to York's Wild Kingdom; hence, they could reschedule observation periods that they missed owing to weather more easily. Additionally, we collected slightly more observations during afternoon/evening at York's Wild Kingdom. As mentioned previously, York's Wild Kingdom was open to the public through September, and visitors were permitted in the fallow deer pen until 18:00 every day. The staff did not feed the deer until after the zoo closed, which may have affected the animals' activity compared to deer in Cooperstown, which did not interact with humans in the same way. However, when we compared data between morning and afternoon/evening periods, we found no differences in activity patterns in the York population.

Another limitation was that we could not control the pZP-treated state of females in either population. Other researchers at Cooperstown were studying the long-term efficacy of pZP immunocontraception; hence, they determined contraceptive status for each female. York's Wild Kingdom is owned privately, and excess fallow deer born in the park are either sold or taken to other facilities in exchange for other species. Therefore, immunocontraception does not fit within the zoo's goals.

Wildlife species benefit if immunocontraception does not affect behavior [Asa, 1996]. Vaccinated individuals continue to display species-typical behavior patterns, herd structure remains intact, and managers can control populations without adverse effects. This study suggests that fallow deer do not display altered activity budgets as a result of contraception, but we encourage additional research over a longer time frame. Some species extend their breeding season when immunocontracepted [Heilmann et al., 1998; Powell, 1999], and we need to determine the consequences, if any. Also, future work should examine activity budgets in populations with more natural sex ratios and under free-ranging conditions.

CONCLUSIONS

1. A fallow deer population containing pZP-treated females did not differ in time spent displaying mating, dominance, or aggressive behavior compared to animals in a nontreated population.
2. Even though pZP-immunocontraception did not adversely affect mating, dominance, or aggressive behavior patterns, future research is required to verify these findings.

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