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THE EFFECT OF IMMUNOCONTRACEPTION ON THE BEHAVIOR AND REPRODUCTION OF WHITE-TAILED DEER

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Abstract: Behavioral and reproductive consequences of porcine zona pellucida (PZP) immunocontraception were examined in a herd of white-tailed deer (*Odocoileus virginianus*; $n = 30$) from September 1992 to September 1994. Does were captured from a wild population and placed within either of 2 large (12-ha total) wooded enclosures. Does were administered either: (1) a single injection containing PZP-emulsified in Freund's complete adjuvant (FCA) and microsphere-encapsulated PZP, (2) 2 injections of PZP emulsified in FCA and Freund's incomplete adjuvant (FIA), 4 weeks apart, or (3) no treatment. Mature, spermic bucks ($n = 5$) were added to each pasture 4 weeks after the final PZP treatment, and reproductive behaviors and fawn production were observed for 2 years. Immunocontracepted females exhibited increased activity compared to non-treated females, presumably reflecting an increased number of estrus intervals. Similarly, enclosure bucks exhibited an extended breeding season compared to males in the surrounding wild population. The 2-injection PZP regimen provided effective contraception during both years of the study. The 1-injection PZP regime provided effective contraception only during the second year, following administration of a PZP booster. Histological evaluation of ovaries failed to reveal among-group differences in ovarian architecture. Contracepted-unpregnant does gained significantly more weight than control females during the study.

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Management of wildlife populations has been a focus for state and federal agencies for more than 50 years, with particular emphasis on the regulation of game populations through selective hunting and trapping. Although there has been increased public sentiment for alternative methods in population management such as trap/relocation (Boyles 1988), drives (Wemmer and Stowe 1995), and implanted steroid contraceptives (Bell and Peterle 1975, Matschke 1977, Levenson 1984), the efficacy of these methods is variable (Turner et al. 1992, Garrott et al. 1992).

Immunocontraceptives also have been used to control reproduction (Kirkpatrick and Turner 1991, Turner et al. 1992, Garrott et al. 1992). In females, the most commonly employed immunocontraceptive agent, PZP (Sacco 1987) stimulates the production of antibodies that sterically inhibit sperm receptors, thereby preventing sperm attachment and conception. Although PZP successfully prevents pregnancy in a diversity of mammalian species (horses: Liu et al. 1989, Kirkpatrick et al. 1990; white-tailed deer: Turner et al. 1992; several exotic ungulate species: Kirkpatrick et al. 1995), the effectiveness and practicality of PZP still requires further validation under actual field conditions. Whether PZP can achieve management objectives of lower population density, while simultaneously providing safe and humane contraception, is unknown.

Reduction of deer density to provide relief for over-browsed vegetation is usually the primary management objective (McShea et al. 1993). In many cases, methods such as hunting already have proven effective for achieving this objective. However, in urban parks and protected areas, hunting may not be feasible or desirable from either a safety or public relations standpoint. In these cases, immunocontraception may provide a suitable alternative method of population control that is safe for both humans and animals. Humane population control has been defined as those approaches that do not (1) cause excessive animal pain and suffering, (2) alter the social organization of the species, and (3) cause permanent loss of reproductive capabilities (Kirkpatrick and Turner 1991). The first assumption is difficult to evaluate, but the second and third assumptions are testable.

Our objectives were to assess the effect of PZP-induced immunocontraception on fecundity, ovarian morphology, and the reproductive behavior and activity patterns of male and female white-tailed deer from mating through parturition in a population consisting of both PZP-treated and control individuals.

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METHODS

The study was conducted at the National Zoological Park's Conservation and Research Center, Front Royal, Virginia (38°N latitude). During August and September 1992, 30 mature does were captured with drop-nets and box traps from a wild population inhabiting a 600-ha forested portion of the center. These does were distributed into 2 partially wooded enclosures (20 and 12 ha). During October 1992, 5 mature bucks were captured with drop-nets, 3 were added to the larger enclosure and 2 to the smaller enclosure. To ensure that all males were producing spermic ejaculates at study onset, we anesthetized and electroejaculated all bucks using a standardized protocol (Monfort et al. 1993). Before addition to the experimental pastures, all animals were weighed, individually marked with numbered eartags, and bled by jugular venipuncture (10 mL).

The PZP vaccine was prepared as described by Liu et al. (1989) and stored frozen. At time of capture, the first experimental group (group-1 does) of 10 does was inoculated with 65 µg of PZP emulsified with 0.5 cc of FCA, described by Kirkpatrick et al. (1990). The inoculations were given intramuscular in the hip or gluteal muscles. About one month after the initial inoculation the 10 does received a second inoculation of 65 µg of PZP + FIA. The second inoculation was administered in the hip region by remote-delivery with self-injecting Pneu-darts (Williamsport, Pa). The second experimental group of 9 does (group-2 does) were given a single inoculation of 65 µg PZP + FCA, which also contained another 65 µg of PZP in timed-release lactide-glycolide microspheres. The microspheres were designed to release the PZP antigen over a 4–6 week period. This dosage also was remotely delivered. The animals of this second experimental group were given a remotely-delivered booster inoculation of 65 µg of PZP + FIA during the second year (Sep 1993). A third group of 11 does (control does) were not administered any PZP. All remote delivery inoculations and boosters were delivered by means of Pneu-dart capture guns from blinds or vehicles.

An equivalent proportion of does from each of the 3 treatment groups were distributed among the 2 pastures. Deer had access of water ad libitum and were supplemented with a total of about 30 kg pelleted ration per week from January through April. Neither visual observations of animals in the pastures, or closer examination of captured does, revealed any evidence of abscesses or lesions at the site of the inoculations. One control doe died during the first winter, and one control doe was removed from the pasture after the first winter because of difficulties in obtaining observation data.

As a behavioral assay of estrus in the females, each buck was observed 5–7 days/week from 1 November, until all males had dropped their antlers (31 Mar 1993 and 1 Mar 1994). A buck was considered to be engaged in mating activity if he was observed either mounting or tending a female. Tending occurred when the male mirrored the activities of a single female, exhibited a flehmen response in conjunction with urination or defecation by the female, and/or defended the female from the approach of other males (Hirth 1977, Marchinton and Hirth 1984).

To determine the length of the mating season for each group of females, the season was divided into 5-day periods starting with the date of the first observed mating. Five days is the maximum period that mating behavior was directed toward an individual female (S. Hakim, pers. obs.). If mating behavior occurred across 2 periods, the female was assigned only to the earlier period. For activity budgets, a female was considered in estrus the day before and after mating attempts. Male and female activity budgets were obtained by observing focal individuals (Altmann 1974) for >30 minute periods. Behavior was classified as walking/running, bedding, or feeding (Kufeld et al. 1988, Beier and Demarais 1994). These daylight observations were conducted throughout the breeding season each year, with 72% beginning within the first 4 hours after dawn. An individual female was not observed twice in one day and each observation period was considered independent. The number of the observation periods did not differ significantly among the 3 experimental groups (e.g., males, contracepted does, control does) with respect to either time of day or month of the year (ANOVA; $F = 0.10$, 2, 14 df; $P > 0.1$ and $F = 0.0$; 2, 14 df; $P > 0.1$).

Fawns were located by searching the pastures every other day during June and July, and every other week through August. Captured fawns were given eartags, which allowed subsequent assignment to a specific female. From June through August, all observed fawns were assigned a mother based on observations of fawns following females, and females directing maternal behaviors toward fawns. Fawn birthdates were placed into 14-day intervals based on motor skills or, if fawns were first seen later in the summer, their size relative to known-age fawns.

In September 1993, 13 does were trapped from the enclosures, weighed, blood sampled, and released back into the enclosures. Between September and October 1994, we captured 18 does, which were anesthetized and ovariectomized using sterile surgical techniques. Whole ovaries and an endometrial biopsy were fixed in 10% buffered formalin for histological examination. Both ovaries from each deer were transected longitudinally then one half was divided into quarters, providing 10 parenchymal surfaces per deer for histologic examination. Ovarian and uterine samples were embedded in paraffin, sectioned at 7 μm, stained with hematoxylin and eosin (H & E), and examined by light microscopy. Histopathologic analyses were performed without knowledge of individual animal treatment. All ovarian sections were examined for the presence of active or regressed corpora lutea, normal zona pellucida development and the presence of inflammatory cells. Quantitative analyses were performed on the median surfaces of all longitudinal sections of ovaries from each deer. The number of healthy and atretic secondary and tertiary follicles, the number of granulosa cell nests (solid aggregations of granulosa cells without an ovum), and the relative abundance of primordial and primary follicles were quantified. Primordial/primary oocyte numbers less than 20 per longitudinal cross section were considered abnormally low. Granulosa cell nests were verified by examination of 2 serial sections of the longitudinally cut surface at 20-μm intervals. Uterine biopsies were evaluated for any abnormalities. Serum titers of anti-PZP antibodies were determined for blood samples collected during autumn 1992, 1993, and 1994 as described by Liu et al. (1989), with some modifications for deer.

For all statistical analysis, significance was considered $P < 0.05$. Before analysis of variance all percentages were first subjected to arcsine transformation. For comparison of percentages, and estrus and parturition dates, we used Wilcoxon signed rank test (Z), or Kruskal-Wallis test (χ^2) for multiple groups (SAS Inst. Inc. 1987). For comparisons of weights and antibody titers, an analysis of variance for repeated measures was used. Quantitative differences in ovarian structures were compared among groups by analysis of variance.

RESULTS

Fawn Production

Within the control group, 9 of 11 does (82%) produced fawns the first year and 8 of 9 does (89%) produced fawns the second year (Table 1). Administration of a 2-injection PZP regimen (group-1) resulted in no offspring production the first year, whereas only 1 out of 10 females (10%) produced fawns the second year. The 1-injection regimen (group-2) did not prevent pregnancy the first year, with 7 out of 9 does (78%) giving birth. Administration of a PZP booster dose to the group-2 does did lower parturition rates the second year, with 2 out of 9 does (22%) producing fawns. Both group-1 and -2 does produced significantly fewer fawns than the control group during the entire study interval ($F = 6.01$, $P = 0.0001$ and $F = 3.17$, $P = 0.003$; Table 1). When the contraceptive failed to prevent pregnancy, the litter size of contracepted does was smaller than control does ($\bar{x}$ = 1.1 and 1.60; $t = 2.45$, $P = 0.027$), primarily because of reduced twinning (10 and 50% twinning). All fawns produced during the study survived through their first winter.

Antibody Titers

Antibody titers for PZP in group-1 contracepted females were significantly higher than control animals 1 and 2 years after contraception (ANOVA; $F = 4.61$, $P < 0.001$ and $F = 4.67$, $P < 0.001$; Table 1). Titers of PZP for group-2 females were not significantly higher than control females one year after contraception ($F = 1.55$, $P = 0.14$), but were marginally higher than control does after 2 years ($F = 1.92$, $P = 0.07$). Not all contracepted females showed increased titers, with 1 out of 6 (17%) group-1 females and 2 out of 5 (40%) group-2 females having low titers after 1 year, and 2 out of 6 (33%) group-2 females having a low titers after 2 years. For the contracepted females, there was a significant negative correlation between titer levels in autumn and the production of fawns the previous summer ($F = 5.98$; 1,

Table 1. Mean (±SE) body weights and antibody titers, and reproductive output, for experimental and control does. For weights and titers, the 1992 values are based on 10 individuals in each group, while 1993 and 1994 values are based on the resampling of 5 individuals in each group.

Experimental group	$\bar{x}$ (±SE) Body weight (kg)			$\bar{x}$ (±SE) Titers of PZP antibodies			% females reproduce		Total fawns produced	
	1992	1993	1994	1992	1993	1994	1993	1994	1993	1994
Control does	45.8 (±1.5)	51.0 (±1.8)	48.9 (±0.7)	5.6 (±0.7)	6.0 (±1.2)	5.6 (±0.7)	82	89	14	11
Group-1 does[a]	41.7 (±3.5)	57.3 (±2.7)	51.3 (±0.6)	8.4 (±2.9)	85.7 (±17.6)	87.2 (±23.7)	0	10	0	1
Group-2 does[b]	44.1 (±1.9)	51.0 (±2.4)	51.2 (±2.7)	5.7 (±0.9)	34.2 (±11.4)	43.3 (±9.3)	78	22	9	2

[a] Group-1 does received 130 μg PZP in yr 1 in 2 injections and no PZP in yr 2.
[b] Group-2 does received 130 μg PZP in yr 1 (half injected and half in microspheres) and 65 μg PZP in year 2.

Table 2. Ovarian histology in white-tailed deer contracepted with porcine zona pellucida vaccination.

Ovarian histology	Control (n = 6)	Group 1[a] (n = 6)	Group 2[b] (n = 6)
Deer with corpora lutea	6 of 6	6 of 6	6 of 6
Deer with <40 primordial follicles	2 of 6	2 of 6	3 of 6
No. of secondary follicles/deer	6.83 ± 1.94[c]	6.2 ± 2.97	11.5 ± 3.67
No. of tertiary follicles/deer	8.67 ± 1.94	6.67 ± 1.45	8.33 ± 1.37
No. of atretic follicles/deer	84.5 ± 13.05	45.83 ± 7.64	71.33 ± 7.68
No. of granulosa cell arrests/deer	0.5 ± 0.34	0.33 ± 0.33	1.33 ± 0.49
Neutrophils in atretic follicles	1 of 6	2 of 6	4 of 6

[a] Group 1 received 130 μg PZP in yr 1 as 2 injections and no PZP in yr 2.
[b] Group 2 received 130 μg PZP in yr 1 (half injected and half in microspheres) and 65 μg PZP in yr 2.
[c] Values represent the group mean ± SE.

16 df, $P = 0.02$, $r^2 = -0.25$). Antibody titers above 50 appear to indicate effective contraception.

Ovary Histology

After 2 years, the ovarian micronanatomy did not differ among treatment groups (Table 2), although considerable within-group variation was noted. All groups had normal folliculogenesis and corpus luteal development. There was a tendency for group-2 deer to have more atretic follicles than group-1 or control deer, but this tendency was not significant and may be a manifestation of more follicular development in that group. More deer in group-2 also had inflammatory reactions (neutrophils) in atretic follicles than group-1 or control deer, but with low group numbers these differences were not significant. Mild suppurative endometritis was noted in 1 unvaccinated deer. No other endometrial lesions were noted.

Weight Gain

There was no significant difference in the initial weight of contracepted and control does (ANOVA: $F = 1.02$, 2 df, $P = 0.37$), but contracepted does gained significantly more weight than control does during the study period (ANOVA repeated measures: $n = 24$, $F = 6.38$, $P = 0.007$). The weight gain was probably due to lower energy demands during lactation, as there was no significant difference in weight between contracepted and control females that both gave birth (ANOVA repeated measures: $n = 14$, $F = 0.04$, $P = 0.49$).

Mating Activity

Males exhibited extended breeding seasons during the first year of the study (Table 3). Mating behavior was observed into March in the larger pasture and into late January in the smaller pasture, with the last antlers cast on 31 March. During the second year, the mating season ended earlier, with the last antler cast on 25 February. However, the second mating season started 17 days earlier than the year before, with first mating seen on 17 November 1993 and 1 November 1994. The date of antler drop for each male was negatively correlated with body weight at start of mating season ($n = 9$, $F = 25.0$, $P = 0.001$, $r^2 = -0.79$). Larger males showed more activity earlier in the season and the staggered dates for antler casting resulted in larger males casting antlers when females were still exhibiting estrous behavior. No mating activity was observed for any males following antler casting.

To determine activity budgets, 351 observation periods totalling 257 hours were conducted over 2 breeding seasons. The activity budget of males was significantly different from that of females (Table 4). Males spent a larger percentage of their time running/walking ($Z = 5.82$, $P < 0.001$), and less of their time feeding ($Z = 3.01$, $P = 0.002$) and bedding ($Z = 1.93$, $P = 0.053$) than females ($n = 182$ and 173 observation periods).

For the does, contracepted females were more active than control females ($Z = 2.34$, $P = 0.02$, $n = 114$ and 53 observation periods; Table 4), but did not spend a significantly different portion of their time feeding ($Z = 0.76$, $P = 0.45$) or bedding ($Z = 1.47$, $P = 0.14$). Increased activity was confined to the days around estrus, as estrous females were more active than non-estrous females (41 and 24%), regardless of experimental group ($Z = 2.48$, $P = 0.012$, $n = 39$ and 138 observation periods). During non-estrous observation periods, contracepted females were not more active than control females ($Z = 1.78$, $P = 0.075$, $n = 91$ and 47 observation periods).

Table 3. The number of females that elicited mating behavior from males during each 5-day period of the breeding season in 1992–93 (A) and 1993–94 (B). Table includes the period of antler drop for the 5 males used in 1992–93 and the 4 males used in 1993–94.

A

	5-Day period during 1992–93 breeding season																
Experimental group	1*	2	3	4	5	6	7	8	9	10**	11	12	13	14	15	16	>16
Control does	0	2	3	1	2	0	0	0	1	1							
Group-1 does[a]	2	4	0	1	1	6	2	0	3	1	0	1	3	0	1	2	3
Group-2 does[b]	5	3	3	2	1	6	3	1	0	2	0	3	1	4			
Antler drop									1		1	1			1		1

* corresponds to 17–21 Nov 1992
** corresponds to 1–5 Jan 1993

B

	5-Day period during 1993–94 breeding season														
Experimental group	1*	2	3	4	5	6	7	8	9	10**	11	12	13	14	>14
Control does	8	2	3	0	0	0	0	1	0	2					
Group-1 does[a]	1	3	2	1	0	1	1	0	2	1	0	0	1		
Group-2 does[b]	2	3	2	1	0	1	1	0	2	1	1	1	0	0	1
Antler drop											1		1	1	1

* corresponds to 1–5 Nov 1993
** corresponds to 16–20 Dec 1993
[a] Group-1 received 130 μg PZP in yr 1 as 2 injections and no PZP in yr 2.
[b] Group-2 received 130 μg PZP in yr 1 (half injected/half in microspheres) and 65 μg PZP in yr 2.

Table 4. The percentage of time spent on activities for each experimental group during the mating seasons of 1992–93 and 1993–94. The number of minutes observed is given in parentheses.

Experimental group	Behavior: Bedding	Feeding	Running–walking
Control does	29 (695)	54 (1278)	16 (436)
Group-1 does[a]	28 (681)	45 (962)	27 (582)
Group-2 does[b]	17 (550)	55 (1546)	25 (704)
Males	17 (1494)	41 (3328)	42 (3157)

[a] Group-1 received 130 μg PZP in yr 1 as 2 injections and no PZP in yr 2.
[b] Group-2 received 130 μg PZP in yr 1 (half injected and half in microspheres) and 65 μg PZP in yr 2.

Based on the behavior of the males, contracepted females exhibited estrous periods later in the season than control females ($Z = 2.75$, $P = 0.006$, $n = 106$ estrous days observed; Table 3). Although administration of the single-dose PZP did not prevent parturition, birthdates were 14–100 days after control does. Parturition dates for contracepted females that did produce fawns were significantly later than the parturition dates of control does ($F = 15.5$; 1, 22 df; $P < 0.001$; Table 5).

DISCUSSION

A 2-injection regimen of PZP was effective for preventing pregnancy in white-tailed deer for up to 2 years after the initial treatments. These 2 doses can be administered before 1 breeding season, or as single injections administered for 2 consecutive years. The 1-injection protocol provided poor contraception efficacy, and, because fawning was delayed, offspring survival might be poor due to reduced overwinter survival. For these reasons, the 1-injection formulation tested is not an appropriate contraceptive treatment. The probability of effective contraception can be determined by measuring serum PZP-antibody titers; levels above 60 provided effective contraception in this study.

Estrous behavior was common within the 2 herds during the breeding season and did end with antler drop by the males, despite the presence of nonpregnant does. However, there were behavioral differences between experimental and control females that can be attributed to the contraception. Contracepted does exhibited estrous behavior for an extended period relative to the control does. In the first year, estrous behavior was seen consistently through late January, with males directing mating behavior toward some females as late as early March. In the second year, mating of contracepted females was observed through January. In general, contracepted does were more active than control does, and the increased activity appeared to be related to estrous behavior. Increased activity, as a result of estrus, has been observed for captive white-tailed deer (Ozoga and Verme 1975), but activity rates for females during the entire rut are not usually higher than rates observed pre- or post-rut (Holzenbein and Schwede 1989). Activity budgets during non-estrous periods were not significantly different between control and contracepted females; therefore, we believe that increased activity rates reflect the fact that conception did not occur at the first or second estrus of the reproductive season.

Activity patterns in white-tailed deer are driven by energy demands (Moen 1976). Whether increased activity every 3 weeks would increase energy demands enough to affect doe health or survival is difficult to evaluate. Adult deer appear relatively immune to most density-dependent factors (Bartmann et al. 1992). However, deer are sensitive to changes in body fat, with 10% reductions in body fat levels during autumn projected to result in a 15% increase in winter mortality (Hobbs 1989). Because supplemental feeding was provided in our study it is impossible to evaluate whether reduced body fat reserves, as a consequence of extended mating activities in contracepted does, might have increased winter mortality. In fact, increased mortality seems unlikely after the first winter since non-pregnant/non-lactating does gained substantial weight during the study interval. Increased body weight in contracepted does during the study presumably reflected better body condition compared to non-

Table 5. The parturition dates of contracepted and control females for 1993 and 1994 (1993/1994).

Experimental group	14-day periods during 93/94 birthing seasons: 1	2	3	4	5	6	7	8
Control does	1/7	6/0	0/0	0/1				
Contracepted does[a]	0/2	1/0	0/0	2/0	2/0	1/1	0/0	1/0

[a] All group-2 does except for a single group-1 doe in 1994.

contracepted animals and this may explain why does exhibited earlier onset of breeding activity during Year 2. A 2-week advance in the onset of breeding has been reported for does in better body condition (McGinnes and Downing 1977).

When PZP-contraception failed to prevent pregnancy, primarily during the first year, females produced fewer fawns and the birthdates of their fawns were significantly delayed. All control does except one fawned within a 3-week interval in late May to early June, a distribution similar to a previous study in Virginia (McGinnes and Downing 1977). This birth synchrony occurred despite the fact that mating behavior was observed over a 10-week period for control does. The mean parturition date for "contraceptive-failure" does was mid-July, with 2 births during the first year recorded after mid-August. Because birth synchrony is known to improve fawn survival for both white-tailed deer (McGinnes and Downing 1977) and mule deer (Odocoileus hemionus, Bowyer 1991), the delayed fawning observed in "contraceptive-failure" would be predicted to affect fawn survival, except in the most favorable habitats or with supplemented food.

Because both pastures contained a mixture of control and experimental does, the study design did not permit evaluation of the effect of the contraception on the males. Analysis of activity budgets inside and outside the breeding season (Hirth 1977, Belyea and Demarais 1994) have shown that the mating season is energetically expensive for males. The length of the mating season observed in this study was about 2 months longer than that reported for males within the population these animals were removed from (Holzenbein and Schwede 1989). However, the extended mating season was not the result of individuals extending their breeding, but rather the staggered mating activity of males within the pastures. Males did reduce their activity levels after casting antlers; antler casting by mature males occurred despite the persistence of younger, antlered males exhibiting mating activity within the study pastures. Supplemental feeding confounded our ability to determine whether an extended mating season would increase mortality rates for the males.

In some species, immunization with PZP in Freund's adjuvant has resulted in ovarian changes that correlate with reduced fertility, such as loss of primordial and primary follicles (dogs and rabbits: Mahi-Brown et al. 1988, Skinner et al. 1984), reduced folliculogenesis (dogs, rabbits, and monkeys: Mahi-Brown et al. 1988, Skinner et al. 1984, Sacco et al. 1991, Upadhyay et al. 1989, Bhatnagar et al. 1992), increased follicular atresia (hamsters, rabbits, monkeys: Hasegawa et al. 1992, Skinner et al. 1984, Upadhyay et al. 1989), and increased granulosa cell nest formation (rabbits, monkeys, hamsters: Skinner et al. 1984, Sacco et al. 1991, Hasegawa et al. 1992). None of these ovarian changes were significantly greater in the PZP-treated deer after 24 months, which corroborates negative pathologic findings in the ovaries of PZP-treated horses (Liu et al. 1989). Contracepted females did exhibit breeding behavior during the second year, which corresponds with the normal functional morphology in their ovaries. However, we cannot exclude the possibility that the observed trends toward more follicular atresia and greater follicular inflammation in deer treated for 2 consecutive years (group-2 does) indicate eventual ovarian atrophy if vaccinations were repeated annually. A similar progression of detrimental effects has been documented in other species (hamsters, rabbits: Hasegawa et al. 1992, Skinner et al. 1984, Jones et al. 1992) and our sample sizes were small for these tests, increasing the probability of Type II error (Taylor and Gerrodette 1993). The continued efficacy of the PZP-contraception for 2 breeding seasons after application to the group-1 does indicates the contraception is not immediately reversible.

The effectiveness of PZP to prevent pregnancy in deer in this trial does not necessarily infer that immunocontraceptives will be effective for regulating all ungulate populations (Garrott 1995). With considerable effort, we were able to successfully complete the remote treatment of wild deer in a natural setting. The remote delivery required a labor-intensive effort and a variety of strategies to get within the 30–40 m necessary to accurately place darts; the most successful strategies included shooting from blinds near bait stations, shooting from a vehicle, and "jacklighting" with a spotlight. The deer in this study were considerably more wild and cautious than most deer in urban settings, for which this form of population control has been designed. The relative habituation of urban deer to humans would make remote-delivery of PZP more feasible. However, we believe this form of delivery would not be feasible for populations outside of the urban or suburban setting, or for populations exposed to hunting pressures and thereby more cautious than these animals.

Beyond logistical considerations, changes in the reproduction of a portion of a population may have compensatory effects on the noncontracepted portion of the population, including increased reproduction and immigration, or reduced emigration and mortality. In fact, it is still not known precisely what demographic traits regulate ungulate populations. Several studies of white-tailed deer imply that fawn survival, and not adult reproduction rates, is the limiting factor on population growth. Increases in fawn production (McCullough 1979), fawn survival during the first months (Dusek et al. 1989, Fuller 1990), or winter mortality of fawns (Bartmann et al. 1992) have all been implicated. Fawn production and survival is compensatory (McCullough 1979, Dusek et al. 1989), with increased production or survival at lower densities. Before implementing management programs that might reduce significantly the female reproductive population, it is essential to consider how the remaining females will respond (Garrott 1995).

MANAGEMENT IMPLICATIONS

This preliminary study indicates that PZP could be an effective contraceptive within controlled circumstances. However, to be a practical contraceptive, most circumstances would demand a single-injection application. Contracepted does exhibited no obvious increase in pain and suffering over control does; over the 2 years of this study the contraception did not cause ovarian damage, but also was not reversible; and the mating and activity behavior was significantly different between control and contracepted does. The changes in activity indicate that food-limited populations may become further stressed by the extended breeding season. For females, this stress may be compensated by the reduced metabolic demands of gestation and lactation. Mating activity of males may be self-limited by endogenous testicular-antler rhythms that ensure a finite breeding season. For both sexes, long-term studies on natural populations are needed to determine the consequences for both individuals and populations.

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