Influences of Hunting on the Behavior of White-Tailed Deer: Implications for Conservation of the Florida Panther

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Abstract: *The effects of deer hunting by humans on deer population dynamics and behavior may indirectly affect the population dynamics and behavior of deer predators. We present data on the effects of hunting on the behavior of white-tailed deer (*Odocoileus virginianus*) on the Osceola National Forest, a potential reintroduction site for the endangered Florida panther (*Felis concolor coryi*). We then use this information to formulate and recommend testable hypotheses to investigate whether these changes in deer behavior influence panther movements, mortality, and hunting success. We monitored 14 radio-collared deer from June 1990 through July 1991 to compare movement, activity, and habitat-use patterns between the hunting and nonhunting seasons. Mean distance of deer to the nearest road, mean distance of activity centers of diel home ranges to the nearest road, and mean nocturnal rate of activity were greater during the hunting than the nonhunting seasons. During the hunting season, deer avoided clearcuts, young pine plantations (4–10 years old), and other open habitats and preferred swamp and mature pine forests, both of which provided cover. These results suggest that deer responded to hunter disturbance by moving away from roads and increasing nocturnal activity. Although recreational deer hunting may reduce the prey base for panthers, the changes we observed in deer behavior during the hunting season may benefit panthers in the following ways: (1) an increase in nocturnal activity and movement away from roads by deer into areas frequented by panthers may increase prey availability for panthers; (2) the movement of deer away from roads may in turn draw panthers away from roads, which may decrease the chance of panthers being killed by vehicular traffic or poachers.*

Influencias de la Cazería en la Conducta del Venado Cola Blanca: Implicaciones en la Conservación de la Pantera de Florida

Resumen: *Los efectos de la caza de venados por humanos en su dinámica poblacional y conducta podría afectar indirectamente las dinámicas poblacionales y conducta de los depredadores de venados. Presentamos datos de los efectos de la cacería en la conducta del venado cola blanca (*Odocoileus virginianus*) en el Bosque Nacional Osceola, un sitio potencial para la reintroducción de la pantera de Florida (*Felis concolor coryi*) amenazada de extinción. Utilizamos esta información para formular y recomendar hipótesis probables para investigar si los cambios en la conducta de los venados influencían los patrones de movimiento, mortalidad y éxito de caza de la pantera. Monitoreamos 14 venados con radio-collares de Junio 1990 hasta Julio 1991 para comparar movimientos, actividad y patrones de uso de hábitat entre las estaciones de caza y caza restringida. La distancia media entre un venado y la carretera más cercana, la distancia media de centros de actividad diurna y la media de la tasa de actividad nocturna fueron mayores durante la estación de caza que durante las estaciones de caza restringida. Durante la temporada de caza, los venados evitaron áreas taladas, plantaciones de pinos jóvenes (4–10 años de edad) y otros tipos de hábitats abiertos, prefiriendo los pantanos y bosques maduros de pino, ambos proveedores de cobertura. Estos resultados sugieren que los venados respondieron a las perturbaciones ocasionadas por la caza alejándose de las carreteras e incre-*

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mentando su actividad nocturna. Aunque la caza recreativa del venado puede reducir la abundancia de esta presa base de las panteras, los cambios observados en la conducta de los venados durante la temporada de caza podría beneficiar a las panteras de las siguientes maneras: (1) un incremento en la actividad nocturna y los movimientos de los venados alejándose de las carreteras hacia áreas frecuentadas por panteras podría incrementar la disponibilidad de presas para las panteras y (2) el movimiento de los venados alejándose de las carreteras podría alejar a las panteras de las carreteras y por lo tanto disminuir la posibilidad de que las panteras sean eliminadas por el tráfico vehicular o por cazadores.

Introduction

The Osceola National Forest (Osceola NF) in northern Florida and the Okefenokee National Wildlife Refuge (Okefenokee NWR) in southern Georgia together constitute one of the top-ranked sites considered for reintroduction of the endangered Florida panther (*Felis concolor coryi*). It served as the location for experimental releases of western cougars (*Felis concolor stanleyana*) in 1988 (Belden & Hagedorn 1993) and 1993 (Jordan 1993). The Osceola NF supports a low-density population of white-tailed deer (*Odocoileus virginianus*) that serves as a recreational base for hunters and may serve as the primary prey base for the Florida panther (Maehr et al. 1990) should reintroduction occur.

The effects of deer hunting by humans on deer population dynamics and behavior (Geist 1970) may indirectly affect the population dynamics and behavior of deer predators such as Florida panthers. Accordingly, knowledge of the effects of hunting is necessary to enhance the effectiveness of both predator and prey management. Hunting is a traditional means of managing deer populations. Although the direct impacts of hunting on deer population dynamics are documented relatively well (McCullough 1979; Nelson & Mech 1986), less is known about its effects on deer behavior. Deer may respond to hunting by using refuges (Kammermeyer & Marchinton 1976; Pilcher & Wampler 1981), avoiding human activity centers (Dorrance et al. 1975; Rost & Bailey 1979), and modifying movement (Marshall & Whittington 1968; Downing et al. 1969), activity (Autry 1967; Vogel 1989), and habitat selection (Swenson 1982; Kufeld et al. 1988). We first present data on the effects of hunting on the behavior of white-tailed deer in the Osceola NF and then use this information to formulate testable hypotheses for investigating whether these changes in deer behavior could influence panther movements, mortality, and predation success.

Methods

The Osceola NF is a 63,631-ha tract in Baker and Columbia counties, Florida, that is characterized by flat terrain, mineral-deficient soils, a warm climate, and pine (*Pinus elliottii* and *P. palustris*) flatwoods vegetation (Harlow & Jones 1965). The density of the Osceola deer population was estimated at 1 per 20 ha (Fritzen et al. 1995) during the period of data collection (June 1990–May 1991). Hunting seasons in the study area were 21 September–6 October (archery hunting, both sexes), 18–25 October (muzzle-loader hunting, males only), and 10 November–5 January (general gun hunting, males only).

Fourteen female white-tailed deer (≥2 years in age) were captured and fitted with motion-sensitive radio collars. Radio locations, estimated by the error-triangle method (Nams & Boutin 1991), were collected according to weekly and diel monitoring schedules. Weekly monitoring involved location of radio-collared deer twice per week during one of eight time periods in a 24-hour cycle such that eight radio locations were obtained monthly, each during a different time period, for each deer during 12 months from June 1990 to May 1991. Time periods were 2 hours before sunrise to sunrise (period 1), sunrise to 2 hours past sunrise (period 2), 2 hours past sunrise to mid-day (period 3), mid-day to 2 hours before sunset (period 4), 2 hours before sunset to sunset (period 5), sunset to 2 hours past sunset (period 6), 2 hours past sunset to midnight (period 7), and midnight to 2 hours before sunrise (period 8). Diel monitoring involved location of 9 of the 14 radio-collared deer at 2-hour intervals during 74 discrete diel periods distributed equally throughout the 12 months from August 1990 to July 1991.

Deer responses to hunting by humans were assessed by means of weekly radio locations and by comparing hunting and nonhunting season measures of (1) distance of deer to nearest road; (2) deer habitat selection; and (3) habitat diversity in areas surrounding deer radio locations. Roads used to measure the distance of deer to the nearest road included interstate highways, paved state and county roads, and graded forest roads over 4 m wide. We determined deer selection of habitats with analyses of use versus availability (Neu et al. 1974). We estimated *observed* utilization (use) of each habitat as the number of radio locations in a given habitat for all deer divided by the number of radio locations obtained for all deer with access to the habitat. We determined

expected utilization (availability) of each habitat by summing the areas of a given habitat occurring within home-range boundaries of all deer and dividing by the sum of the areas of home ranges of all deer with access to the habitat. The diversity of habitats surrounding deer radio locations was estimated by summing the number of habitats contained within a 12.6-ha circle (200-m radius) centered on each radio location. Habitats available were (1) SWAMP, cypress (*Taxodium* spp.), bay (*Nyssa* spp.), and creek swamps (26.4%); (2) CLRCT, recent clearcuts containing planted pine, 0–3 years (8.2%); (3) SAPLG, young plantations containing pine saplings, 4–10 years (4.8%); (4) IMMTM, immature pine timber, 11–30 years (13.5%); (5) MATTM, naturally regenerated or planted pine, over 30 years (46.1%); and (6) OTHER, roads, railroads, and rights-of-way (1.0%).

Deer responses to hunting were assessed by means of diel monitoring by comparing hunting- and nonhunting-season measures of (1) diel home range size, derived using the minimum convex polygon method (Mohr 1947); (2) distance between diel home range activity center, taken as the arithmetic center of activity for a diel home range, and the nearest road; (3) diel home range activity center to diel radio-location distance; and (4) diel, diurnal, and nocturnal deer activity, estimated by dividing the number of active radio locations obtained during a diel monitoring session (or diurnal-nocturnal subset) by the total number of radio locations obtained during that session (or subset). Deer activity status was estimated based on fluctuations in radio signal strength and pulse frequency. Diurnal and nocturnal time periods included those in which humans were most likely (periods 1, 2, 3, 4, 5, and 6) and least likely (periods 7 and 8) to be present.

We compared mean measures of habitat diversity and deer activity between hunting and nonhunting seasons (all hunting seasons combined) and between diurnal and nocturnal time periods using either paired-difference t tests for normally distributed data or Wilcoxon signed-rank tests for nonnormally distributed data. Habitat selection was determined via construction of 95% confidence intervals about observed habitat utilization proportions and comparison to expected utilization proportions (Neu et al. 1974). Expected utilization proportions exceeding the upper confidence limit of observed proportions denoted avoidance, whereas expected proportions less than the lower confidence limit of observed proportions denoted preference.

Results

The mean distance of deer to the nearest road differed between hunting and nonhunting seasons and between diurnal and nocturnal periods (Table 1). Females were located further from roads during the hunting season than during the nonhunting season (sign rank = 4.587, df = 13, p = 0.001). Mean distance of females from roads did not differ between diurnal and nocturnal time periods of the hunting season (t = 1.541, df = 13, p = 0.150), but females were located further from roads diurnally than nocturnally during the nonhunting season (t = 2.190, df = 13, p = 0.047).

Diel home-range characteristics differed between hunting and nonhunting seasons (Table 1). Mean diel home range size did not differ between hunting and nonhunting seasons (t = 1.325, df = 8, p = 0.222). Activity centers of diel home ranges, however, were located further from roads during the hunting season than during the nonhunting season (t = 3.159, df = 8, p = 0.013). Also, mean distance between diel activity centers and diel ra-

Table 1. Measures of movement, activity, and habitat selection for radio-collared female white-tailed deer (n = 14), Osceola National Forest, Florida, June 1990–July 1991.[a]

	Hunting season			*Nonhunting season*		
Measurement	*diel*	*diurnal*	*nocturnal*	*diel*	*diurnal*	*nocturnal*
Distance						
Deer to road (m)[b]	396.0	411.7	351.9	345.0	355.4	320.9
Activity center to road (m)[c]	419.7	n.a.	n.a.	366.6	n.a.	n.a.
Activity center to deer (m)[d]	264.7	253.3	276.2	249.4	232.9	265.8
Home range size (ha)[e]	26.4	n.a.	n.a.	21.7	n.a.	n.a.
Rate of activity (%)[f]	53.2	44.8	63.7	54.9	53.5	57.1
Habitat diversity[g]	1.9	1.9	1.9	2.1	2.1	2.1

[a] *Hunting season included the periods 21 September–6 October 1990, 18–25 October 1990, and 10 November 1990–5 January 1991. Nonhunting season included the periods 1 June–20 September 1990 and 6 January–30 May 1991. n.a.: not available.*
[b] *Mean distance (m) from radio-collared deer to the nearest road.*
[c] *Mean distance (m) from arithmetic centers of activity of diel home ranges to the nearest road.*
[d] *Mean distance (m) from arithmetic centers of activity of diel home ranges to radio locations defining the home range.*
[e] *Mean size (ha) of diel home ranges as determined by the minimum convex polygon method.*
[f] *Mean rate of activity (number of active radio-locations/total number of radio locations) obtained during diel monitoring of radio-collared deer.*
[g] *Mean number of habitats contained within 12.6-ha circles encompassing radio locations obtained during monthly monitoring of radio-collared deer.*

dio locations did not differ between diurnal and nocturnal periods during the hunting season ($t = 0.990$, df = 8, $p = 0.351$), but mean nocturnal distance exceeded mean diurnal distance during the nonhunting season ($t = 3.414$, df = 8, $p = 0.009$).

Mean diel rate of activity did not differ between hunting and nonhunting seasons ($t = 0.645$, df = 8, $p = 0.537$; Table 1). Mean nocturnal rate of activity exceeded the mean diurnal rate during the hunting season ($t = 3.221$, df = 8, $p = 0.012$) but not during the nonhunting season (sign rank = 4.5, df = 8, $p = 0.652$). Mean diurnal rates of activity did not differ between hunting and nonhunting seasons (sign rank = 15.5, df = 8, $p = 0.074$), but mean nocturnal rate of activity during the hunting season exceeded that during the nonhunting season ($t = 3.250$, df = 8, $p = 0.012$).

Both habitat selection (Table 2) and diversity of habitat complexes occupied (Table 1) by deer differed between hunting and nonhunting seasons. During the nonhunting season, deer avoided SAPLG and preferred IMMTM habitats ($p < 0.05$). During the hunting season, CLRCT, SAPLG, and OTHER habitats were avoided, whereas SWAMP and MATTM habitats were preferred ($p < 0.05$). Habitat diversity of 12.6-ha circles surrounding deer radio locations during the nonhunting season exceeded that during the hunting season ($t = 2.462$, df = 13, $p = 0.029$).

Discussion

Behavior of female white-tailed deer on the Osceola NF differed between hunting and nonhunting seasons. Although factors such as rut (Fritzen 1992), changing nutritional quality and quantity of food resources (Byford 1969; Kilgo & Labisky 1997), and the presence of stray hunting dogs (Progulske & Baskett 1958; Sweeney et al. 1971) probably influenced behavior during the hunting season, deer also apparently responded to human hunting activity. Unfortunately, we were unable to monitor movements of nonhunted deer (i.e., control population) on the study area because no such refugia were available. Studies elsewhere that have compared movements of hunted and nonhunted populations, however, have demonstrated that deer in hunted populations exhibit greater mobility than those in nonhunted populations (Root et al. 1988; Labisky et al. 1995).

Deer have responded to human hunting by either shifting home ranges (Zagata & Haugen 1973; Kammermeyer & Marchinton 1976) or remaining in pre-hunt home ranges (Marshall & Whittington 1968; Kufeld et al. 1988; Sargent 1992). Deer on the Osceola NF shifted diel home ranges away from roads during the hunting season and thereby avoided areas of greater human activity. Hunter activity on the study area was concentrated principally within 200 m of roads. Therefore, because of the density of understory vegetation on the Osceola NF, the relatively small shift in diel home ranges away from roads likely was adequate to reduce the disturbance of deer by hunter-related activities. Also, deer moved toward roads during the nocturnal periods of the nonhunting season but did not do so during the hunting season. Collectively, these findings suggest that human disturbance was sufficiently strong to affect diel movement during the hunting season but not during the nonhunting season.

Table 2. Habitat selection by radio-collared female white-tailed deer ($n = 14$), Osceola National Forest, Florida, June 1990–May 1991.

Season[a]	*Habitat*[b]	*Number of observations*	P_{io}[c]	P_i[d]	*Confidence interval*[e] ($\leq P_i \leq$)	*Selection*[f]
Hunting						
	SWAMP	138	0.346	0.389	0.362, 0.416	prefer
	CLRCT	5	0.051	0.014	0.007, 0.021	avoid
	SAPLG	19	0.089	0.054	0.041, 0.067	avoid
	IMMTM	68	0.194	0.192	0.170, 0.214	no selection
	MATTM	124	0.313	0.349	0.323, 0.375	prefer
	OTHER	1	0.007	0.003	0.000, 0.006	avoid
Nonhunting						
	SWAMP	291	0.315	0.326	0.300, 0.352	no selection
	CLRCT	19	0.023	0.021	0.013, 0.029	no selection
	SAPLG	53	0.097	0.059	0.046, 0.072	avoid
	IMMTM	210	0.205	0.235	0.211, 0.259	prefer
	MATTM	316	0.355	0.354	0.327, 0.381	no selection
	OTHER	5	0.006	0.006	0.002, 0.010	no selection

[a] *Hunting season and nonhunting seasons are defined in Table 1.*
[b] *SWAMP: bay, cypress, and creek swamps; CLRCT: planted pine, 0–3 years; SAPLG: planted pine, 4–10 years; IMMTM: planted pine, 11–30 years; MATTM: pine over 30 years; and OTHER: roads, railroads, and rights-of-way.*
[c] P_{io} *denotes the expected proportion of habitat use.* P_{io} *values less than the lower confidence limit denote preference.* P_{io} *values greater than the upper confidence limit denote avoidance.*
[d] P_i *denotes the observed proportion of habitat use.*
[e] *The 95% confidence intervals constructed about* P_i.
[f] Prefer *and* avoid *denote significance* ($p < 0.05$). *No selection denotes lack of significance* ($p > 0.05$).

Autry (1967) and Nixon et al. (1991) determined that deer responded to human hunting disturbance by decreasing diurnal activity and seeking cover. Activity patterns of deer on the Osceola NF support their conclusions. Nocturnal activity exceeded diurnal activity during the hunting season but not during the nonhunting season. Furthermore, although diurnal activity did not differ between hunting and nonhunting seasons, deer tended to exhibit lower diurnal activity during the hunting season than during the nonhunting season. Also, nocturnal activity was greater during the hunting season than during the nonhunting season. These results suggest that deer responded to human hunting by decreasing diurnal activity and, compensatorily, increasing nocturnal activity.

Consistent with previous research (Marshall & Whittington 1968; Swenson 1982; Kufeld et al. 1988), deer on the Osceola NF altered habitat-selection patterns during the hunting season. Deer were relatively nonselective during the nonhunting season, avoiding old-field habitats and preferring 11- to 30-year-old pine habitats. During hunting season, however, selectivity increased as deer avoided clear-cut, old-field, and other habitats and preferred swamp and pine over 30 years old. Clear-cut, old-field, and other habitats likely were avoided because (1) the general lack of cover in these habitats rendered deer more vulnerable to harvest and (2) these habitats, if not actually consisting of roads or other human disturbance habitats, occurred near roads where hunters concentrated their efforts. Similarly, deer likely preferred swamp and mature timber because these habitats were well removed from roads and logged areas and contained abundant cover. We do not believe that the preference for swamps was attributable to the availability of oak (*Quercus* spp.) mast, which was coincident with the hunting season, because oaks were present in only a few of the swamps used by the radio-collared deer (personal observation), yet deer increased their use of all swamps, not just those containing oak mast.

In addition to increased selectivity of their habitats, deer on the Osceola NF occupied less diverse habitat assemblages during the hunting season than during the nonhunting season. This finding likely resulted from deer avoiding roaded and recently logged areas during the hunting season, concurrent with increased use of large, homogenous blocks of mature pine and swamp habitats.

Effects of Deer Behavior on Panthers

We suggest that the altered behavior patterns of deer during the hunting season may have important implications for the potential reintroduction of the Florida panther to the Osceola NF–Okefenokee NWR region. Although human hunting for deer may reduce the overall prey base for panthers, behavioral responses of deer to human hunting may be partially offsetting for the following reasons. First, Belden and Hagedorn (1993) found that western cougars released on the Osceola NF in 1988 established home ranges that followed major drainages and included relatively few roads. The tendency for deer to move away from roads during the hunting season and to prefer relatively roadless blocks of mature pine and swamp habitat may enhance panther hunting success by increasing prey concentrations in areas preferred by panthers. Second, the nocturnal nature of deer during the hunting season also may enhance the hunting success of panthers, largely nocturnal predators, because increased nocturnal activity of deer likely results in increased movement and, therefore, increased probability of detection by panthers. Finally, if panthers respond to shifting distributions of their prey base, the increased avoidance of roads by deer may concurrently diminish the frequency of panther occurrence near roads, reducing both the probability of panther-vehicle collisions, a principal cause of death for Florida panthers (Maehr et al. 1991), and human sightings, which can facilitate indiscriminate killing of panthers (Belden & Hagedorn 1993). The presence of deer hunters in the forest may not constitute as great a risk to panthers as do vehicles and the type of indiscriminate poaching typically conducted from vehicles. Whether the hypothesized survival benefits derived from these mechanisms are sufficient to offset the potentially greater risk presented by hunters in the forest is an unanswered question.

Given these possibilities, we propose that future panther research address the following two testable hypotheses regarding the interactions among hunters, deer, and panthers. First, if deer both move away from roads—and therefore into panther home ranges—and become more nocturnal, then we predict that hunting success by panthers should be greater during the hunting season than during the rest of the year. Second, if panthers follow deer movements and thereby avoid roads, we predict that panther mortality due to panther-vehicle collisions and poaching should be lower during deer season than during the rest of the year. It should be established prior to testing these hypotheses that deer behavior in the presence of both hunters and panthers does not differ from behavior in the presence of hunters only.

It will not be easy to pursue reliable tests of these hypotheses for the Osceola study area because of the small sample size of cougars and the need for long-term data on cause-specific cougar mortality patterns. Therefore, we suggest that existing data from deer and Florida panther research conducted in areas open to public hunting, such as the Big Cypress National Preserve, might be used to test these hypotheses. Finally, to test whether the potential indirect effects of deer hunting have any effect on the long-term survival of panthers, we suggest comparing survival rates of panther populations living in

areas subjected to deer hunting with those of populations in areas closed to deer hunting.

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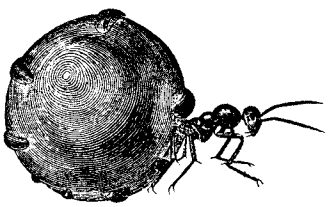
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