

MULE DEER MOVEMENTS IN RESPONSE TO MILITARY ACTIVITY IN SOUTHEAST COLORADO

THOMAS R. STEPHENSON,¹ Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060, USA

MICHAEL R. VAUGHAN, Virginia Cooperative Fish and Wildlife Research Unit, National Biological Service, Blacksburg, VA 24061, USA

DAVID E. ANDERSEN,² U. S. Fish and Wildlife Service, Colorado Fish and Wildlife Assistance Office, 730 Simms Street, Golden, CO 80401, USA

Abstract: During January 1986–September 1988 we studied the behavioral responses of 71 radiocollared mule deer (*Odocoileus hemionus*) to military activity on the Piñon Canyon Maneuver Site in southeastern Colorado. Military training was initiated on the site during August 1985 and recurred about 3 times yearly for periods of one month. During a maneuver, $\frac{1}{4}$ of the site was used for training in accordance with a rotational land use schedule. During the nonsummer seasons, female seasonal convex polygon and harmonic mean home ranges were larger in maneuver and previous-maneuver areas than nonmaneuver areas ($P < 0.002$). During summer, female convex polygon home ranges were larger in maneuver than nonmaneuver areas ($P = 0.066$). Fawn summer home ranges were larger in maneuver than previous-maneuver areas ($P < 0.01$). Male home range sizes differed only for 50% harmonic mean transformation annual home ranges ($P = 0.056$); bucks in maneuver areas had larger home ranges than in nonmaneuver areas. Female deer in maneuver areas exhibited significant home area shifts ($P = 0.049$) between premaneuver and maneuver periods more frequently (40.0%) than did deer in nonmaneuver (control) areas (12.5%). Mule deer in military training areas may have responded to human harassment, alteration of security cover, or destruction of the forage base. We suggest that deer may respond more intensely to unpredictable than predictable human activity.

J. WILDL. MANAGE. 60(4):777–787

Key words: Colorado, disturbance, home range analysis, military activity, movements, mule deer, *Odocoileus hemionus*.

To manage ungulate populations subjected to human activities, ungulate responses to these activities first must be assessed. Studies designed to assess the effects of human activity on white-tailed deer (*Odocoileus virginianus*) (Dorrance et al. 1975, Eckstein et al. 1979), mule deer (Freddy et al. 1986, Merrill et al. 1994), elk (*Cervus elaphus*) (Edge et al. 1985, Peek and Hieb 1976), caribou (*Rangifer tarandus*) (Calef et al. 1976, Shideler et al. 1986), and mountain sheep (*Ovis canadensis*) (MacArthur et al. 1982) concluded that recreation, development, mining, logging, and military activity may negatively affect these ungulates. The short-term behavioral responses exhibited by individual ungulates in response to human activity may have negative long-term population implications if

sustained. Harassment acts as a stressor, which might increase mortality or decrease fecundity.

During 1983–84, before initiation of military activity, Gerlach (1987) obtained baseline population data on mule deer for use in developing a comprehensive wildlife management plan for the U. S. Army's Piñon Canyon Maneuver Site (PCMS), Colorado (Fig. 1). Subsequently, this study was designed to assess the effects of military training activity on the behavior of PCMS mule deer. The objectives were to (1) quantify the level of military activity on the maneuver site, and (2) determine whether mule deer alter home range size and fidelity in response to observed levels of military training activity.

We thank A. Archuletta, S. R. Browning, A. Fowler, M. Lane, M. Lentsch, D. Middlebrook, J. Sanborn, and A. W. Stephenson for field assistance. C. Bandy, S. R. Emmons, W. R. Mytton, A. P. Pfister, B. D. Rosenlund, and T. L. Warren coordinated and assisted in phases of the study. M. Canestorp, R. L. Kirkpatrick, and D. F. Stauffer provided comments on the manuscript. This project was funded by the Environment, Energy, and Natural Resources Division

¹ Present address: Alaska Department of Fish and Game, Moose Research Center, 34828 Kalifornsky Beach Road, Suite B, Soldotna, AK 99669, USA.

² Present address: Minnesota Cooperative Fish and Wildlife Research Unit, National Biological Service, Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108, USA.

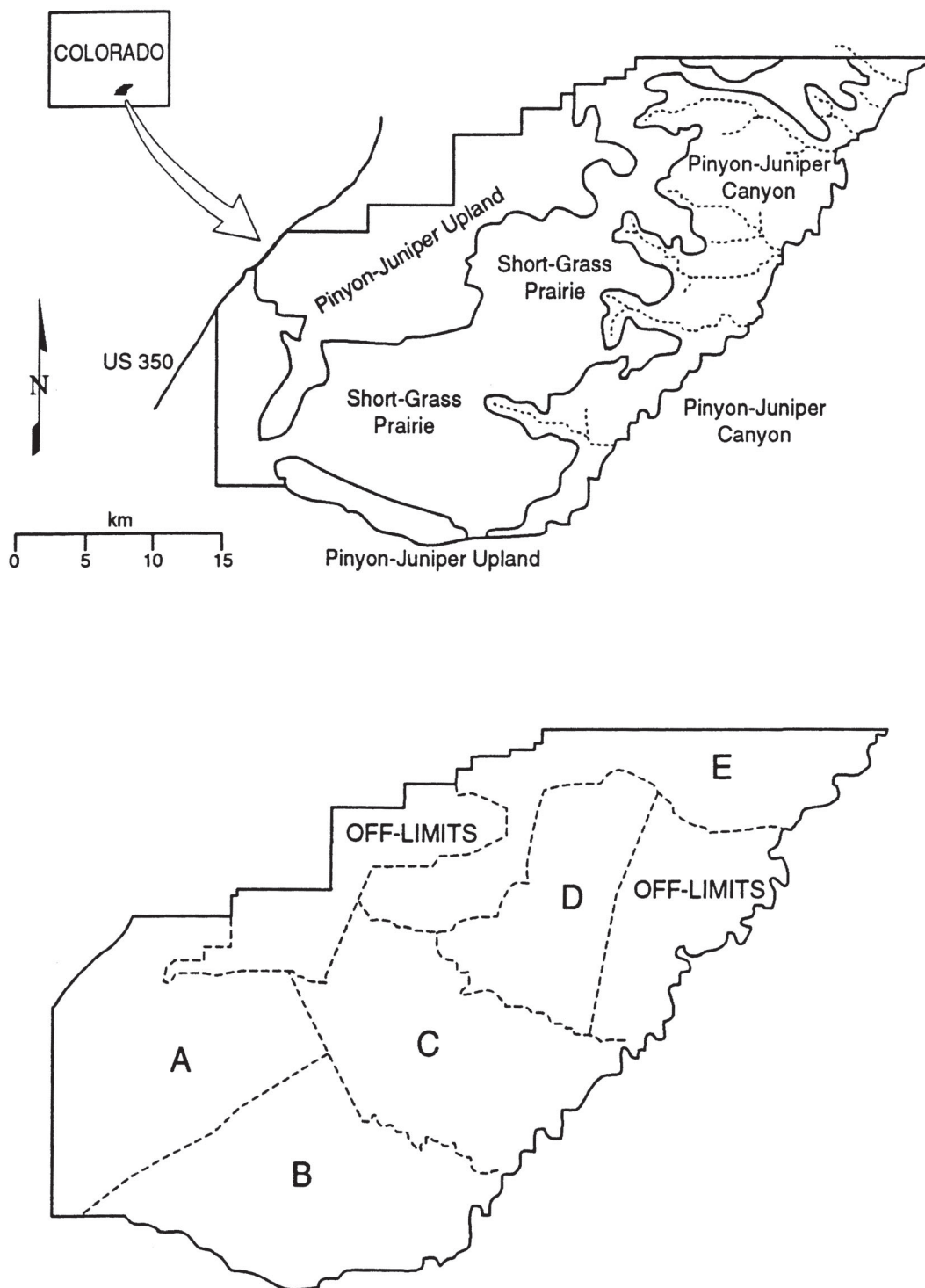


Fig. 1. Top: The Piñon Canyon Maneuver Site in southeast Colorado. Bottom: Locations of 5 maneuver sectors (A-E) and 2 off-limits areas (i.e., no land-based military training) on Piñon Canyon Maneuver Site, Colorado.

of the U.S. Army, Fort Carson, Colorado; the Virginia Cooperative Fish and Wildlife Research Unit, National Biological Service; Fish and Wildlife Assistance Office, U.S. Fish and Wildlife Service, Golden, Colorado; and the Department of Fisheries and Wildlife Science, Virginia Polytechnic Institute and State University.

STUDY AREA

The 1,040 km² PCMS lies along the Purgatoire River in Las Animas County, Colorado, about 64 km northeast of Trinidad in the Great Plains Physiographic Province (U. S. Dep. Army 1980). The site was broad-sloping shortgrass prairie dissected by rocky canyons and breaks to the east and southeast, and bordered by pinyon-juniper (*Pinus edulis-Juniperus monosperma*) uplands to the north, northwest, and southwest (Fig. 1). Elevations ranged from 1,311 to 1,737 m. Mean annual precipitation was 30–40 cm and mean monthly temperatures ranged from –1 C in January to 23 C in July.

Vegetation on the PCMS consisted primarily of shortgrass prairie and pinyon-juniper woodland communities (Kendeigh 1961). Shortgrass prairie was dominated by blue grama (*Bouteloua gracilis*), in association with galleta (*Hilaria jamesii*), ring muhly (*Muhlenbergia torreyi*), western wheatgrass (*Agropyron smithii*), broom snakeweed (*Xanthocephalum sarothrae*), sand dropseed (*Sporobolus cryptandrus*), and Bigelow sage (*Artemisia bigelovii*). In addition to pinyon-juniper, the woodlands included grasses and forbs such as blue grama, sand dropseed, galleta, needle-and-thread (*Stipa comata*), and broom snakeweed. Shrub species present were mountain mahogany (*Cercocarpus montanus*), fourwing saltbush (*Atriplex canescens*), skunkbush sumac (*Rhus trilobata*), currant (*Ribes* spp.), and rabbitbrush (*Chrysothamnus nauseosus*).

The predominant land use on the PCMS historically was dry-land cattle and sheep grazing; however grazing was discontinued in 1984. In August 1985, military training began on the site and through 1988, recurred about 3 times yearly for periods <1 month. In accordance with a rotational land use schedule, 3 of 7 sectors on the site were used for training during any given maneuver (Fig. 1).

METHODS

We captured adult mule deer in Clover traps (Clover 1956), by drop-net (Ramsey 1968), or

with a Coda net gun (Coda Enterprises, Mesa, Ariz.). We baited Clover traps with apple pulp and manually restrained captured deer. We also baited drop-nets with apple pulp, and used them on open plateaus. We captured deer with Coda net guns fired from a Bell Soloy helicopter (Barrett et al. 1982) after hazing them into suitable terrain (e.g., bare slopes, woodland openings, or open grassland); hazing was limited to 15 minutes. We marked captured deer with numbered color eartags and frequency-specific, color-coded radiocollars (164–165 MHz; 540 g; Adv. Telem. Systems, Inc., Bethel, Minn.). Radiocollars for bucks were large enough to accommodate neck swelling during the rut. We identified deer age classes (fawn, yrl, and ad) by tooth replacement and wear (Robinette et al. 1957).

During June and July, we located newborn fawns by ground surveillance of radiocollared and unmarked does, and captured them by hand. If fawns were still moist with amniotic fluid when located, they were not handled or collared until the following day. We equipped captured fawns with expandable break-away radiocollars (135 g) (Trainer et al. 1981) and numbered button eartags and recorded their sex, weight, and general condition. We estimated ages and birthdates according to Robinette et al. (1973).

We located radiocollared deer with a handheld, 2-element “H” antenna and pinpointed locations by visual observation, circling the animal (mean radius of 50–100 m), or triangulation with multiple directional bearings. Circling was the predominant technique, followed by visual observation. We obtained less than 5% of locations by triangulation; 75% of these used ≥3 directional bearings taken within a 20-minute period at a distance of <1 km. We estimated telemetry accuracy by locating 22 transmitters placed in locations unknown to us, but ≤2 km distant from bearing stations; 86% of fixes estimated from bearings were accurate to within 100 m of the true location and average error polygon size was 2 ha. We used triangulation primarily at night. We supplemented ground locations with weekly or biweekly locations from a helicopter or fixed-wing aircraft with 2 2-element “H” antennae on opposite sides of the aircraft. We plotted all locations on U. S. Geological Survey 1:24,000 topographic maps and recorded Universal Transverse Mercator grid coordinates to the nearest 100 m. We located radiocollared adults and fawns >2 months every 1–10 days and fawns ≤2 months every 1–3 days.

We calculated seasonal and annual home ranges with the minimum convex polygon (Hayne 1949) and harmonic mean transformation (HMT) (Dixon and Chapman 1980) methods. Each home range estimation technique provided unique information. The convex polygon was valuable because infrequent outlying points, which probably occurred in response to military activity, illustrated increased movement and increased energy expenditure (Freddy et al. 1986). The 95% HMT estimator described the area used by an individual without being heavily influenced by infrequent extreme outlying locations. The 50% HMT home range size represented a core area used most intensively by an animal. Differences with each of the 3 estimators were important because they illustrated short-term (convex polygon), and long-term (50% HMT) responses to human activity. We used a 10×10 grid size with a 2.0 scaling factor in calculating the harmonic mean home ranges (Samuel et al. 1985). We determined the minimum sample size for home range analysis with observation-area curves (Odum and Kuenzler 1955). We compared home range sizes among 3 treatment conditions: maneuver, previous-maneuver, and nonmaneuver (control). We defined maneuver areas as sectors in which a maneuver occurred during a given season, previous-maneuver areas as sectors in which a maneuver had occurred during a previous, but not the current season, and nonmaneuver areas as areas in which no training had occurred and was not currently occurring. Maneuvers were rotated among sectors of the site, thus individual deer had seasonal home ranges in each of the 3 types of areas. We included multiple home ranges of individual deer in the analysis because factors, such as military training conditions, that dictate home range size differed among seasons. Furthermore, because Gerlach (1987) found no difference in home range size among different topographic areas of the site before military training activity, we directly compared home range size in maneuver, previous-maneuver, and non-maneuver areas. We calculated only summer and fall home ranges for fawns, and because of small sample size, excluded the nonmaneuver category in fawn home range analysis.

We used Gerlach's (1987) definition of seasons on PCMS as defined by mule deer behavior. Winter (1 Jan–15 Mar) began with the end of the rutting season and continued through antler shedding and the formation and break-up of

winter groups; spring (16 Mar–31 May) was the prefawning period after break-up of family groups; summer (1 Jun–15 Sep) was the fawn rearing period; and fall (16 Sep–31 Dec) encompassed the rut.

We analyzed summer home ranges of does and fall home ranges of bucks separately because, in each case, they were significantly larger than home ranges during all other seasons, when home range size was similar. Therefore, the nonsummer and nonfall periods for does and bucks, respectively, included seasonal home ranges, which were pooled for the overall analysis. We used the Kruskal-Wallis multiple range test to test for differences in home range size. If Kruskal-Wallis analysis indicated a difference, we conducted a nonparametric protected Fisher's Least Significant Difference (LSD) test to determine which treatment was different. Because of the small sample sizes in many of the analyses, $\alpha = 0.1$ was used to indicate statistical significance. When the result of a Kruskal-Wallis or Wilcoxon Rank Sum test was nonsignificant, we analyzed the statistical power of the test's parametric equivalent.

We examined home area fidelity (the tendency of a deer to remain in a previously occupied area during different periods of time) of females only, by closely monitoring individual does in nonmaneuver sectors and sectors subject to military maneuvers during a 3-week period immediately before training and during the 3-week training period. During both 3-week periods we located deer every 2–4 days. In contrast to home ranges, home areas (or use areas) contained fewer points than required to define a meaningful home range, but represented the areas used during each of the 3-week periods noted above. To test for locational shifts (movement from 1 use area to another), we compared distances between within-group pairs of pre-maneuver and maneuver period locations to distances between ungrouped locations for an individual using multi-response permutation procedures (MRPP) (Mielke et al. 1976). MRPP is a nonparametric statistical test that permits comparison of animal location distributions but does not assume that data are normally distributed; instead, a null distribution is defined with all possible permutations of the observations (Mielke et al. 1976). Anderson (1988) noted that the *P*-values associated with each pair of monitoring periods denote the probability that the distribution of the animal's locations were not

Table 1. Tactical vehicle maneuver statistics for the Piñon Canyon Maneuver Site, Colorado, January 1986–September 1988.

Maneuver	Dates	Occupied sectors	No. personnel ^a	No. wheeled vehicles ^a	No. tracked vehicles ^a
1986					
Winter	25 Feb–7 Mar	A, B, C	2,951	483	371
Summer	8–29 Jul	A, B, C	3,789	949	309
Fall	20 Oct–7 Nov	A, B, C	3,290	771	495
1987					
Spring	13 Mar–1 Apr	B, C, D	6,619	1,833	564
Fall	23 Oct–9 Nov	C, D, E	3,108	406	503
1988					
Winter	25 Jan–20 Feb	C, D, E	5,900	1,000	485
Summer	12 Jul–5 Aug	A, B	2,624	730	401

^a These data are estimates from Movement Control Center, PCMS and Fort Carson, Colorado.

different between periods. We further tested for a difference in the proportion of deer exhibiting significant locational shifts between nonmaneuver and maneuver areas using a Z-test.

We also used MRPP to determine the average distance between locations for each doe during the premaneuver and maneuver 3-week periods. This value was an index to movement during the period over which an individual was monitored.

We monitored troop movements, land-based vehicular traffic, aerial traffic, and military activity daily while tracking deer. Weekly aerial telemetry flights helped identify military traffic and encampments. We identified active encampments and movements that were not observed by disturbance to the landscape (i.e., fresh tank tracks, trash, and destroyed vegetation). We obtained numbers of troops and tactical vehicles/maneuver from Movement Control (PCMS and Fort Carson, Colo.).

RESULTS

Military Activity

Seven 2- to 3-week training maneuvers occurred during January 1986–September 1988 (Table 1). Number of personnel per training exercise ranged from 2,624 to 6,619 and the total number of vehicles on site at 1 time was between 854 and 2,397. Before 13 March 1987 and 23 October 1987, no training had occurred in sectors D and E, respectively. Two control areas were officially off-limits and no training occurred in these areas throughout the study (Fig. 1). We could not obtain actual numbers of helicopters and other aircraft on site at the same time, but estimated that the normal range was from 30 to 50. In general, helicopters tended to

operate in proximity to land-based vehicular training.

Home Range Size

We calculated home ranges for 71 mule deer (2,994 telemetry locations) with sufficient locations ($\bar{x} = 20$) for each seasonal home range analysis based on observation-area curves (Odum and Kuenzler 1955). We found no relation between number of locations/individual and home range size of individuals ($r = 0.01$, 145 df, $P = 0.22$).

Mean seasonal home range size of does on PCMS during fall, winter, and spring differed ($P < 0.002$) among military training conditions (Table 2). For each home range analysis (e.g., convex polygon, HMT), home ranges were larger in maneuver ($n = 26$) and previous-maneuver ($n = 5$) areas than nonmaneuver areas ($n = 17$). Sizes of home ranges in maneuver and previous-maneuver areas were similar ($P > 0.43$). Size of summer home ranges of does differed among area condition with the convex polygon technique only ($P = 0.066$); maneuver area ($n = 21$) home ranges were larger ($P = 0.033$) than nonmaneuver area ($n = 10$) home ranges, but previous-maneuver area ($n = 11$) home ranges did not differ from either maneuver ($P = 0.14$) or nonmaneuver areas ($P = 0.53$). Trends in annual female home range sizes were similar to seasonal trends, but only 95% HMT home ranges were different ($P = 0.008$) among military training conditions. Maneuver ($n = 33$, $P = 0.003$) and previous-maneuver ($n = 6$, $P = 0.02$) area home ranges were larger than nonmaneuver area home ranges ($n = 13$); maneuver and previous-maneuver area home ranges were similar ($P = 0.98$). The statistical power of nonsignificant summer and annual analyses comparing doe home range

Table 2. Mean (SE) seasonal and annual home range size of radiocollared adult female mule deer by training conditions on the Piñon Canyon Maneuver Site, Colorado, January 1986–September 1988.

Period	Area conditions	n	Convex polygon (km ²)	50% HMT (km ²)	95% HMT (km ²)
Non-summer (fall, winter, spring)	Maneuver	26	8.26 (1.34) A*	2.24 (0.29) A	16.08 (3.48) A
	Previous-maneuver	5	6.96 (2.51) A	1.64 (0.43) A	14.44 (7.20) A
	Nonmaneuver	17	2.30 (0.30) B	0.77 (0.09) B	3.80 (0.39) B
Summer	Maneuver	21	9.71 (2.12) A	2.08 (0.51) A	17.13 (4.86) A
	Previous-maneuver	11	5.44 (0.99) AB	1.22 (0.14) A	7.91 (1.42) A
	Nonmaneuver	10	4.58 (0.88) B	1.15 (0.33) A	7.69 (1.57) A
Annual	Maneuver	33	18.82 (2.27) A	4.51 (0.53) A	26.63 (2.52) A
	Previous-maneuver	6	18.93 (3.30) A	4.45 (0.90) A	24.80 (4.00) A
	Nonmaneuver	13	12.21 (1.66) A	2.94 (0.58) A	14.16 (1.70) B

* Means within the same column and period that share the same letter are not significantly different ($P > 0.1$) according to nonparametric protected LSD.

sizes among training conditions was between 0.17 and 0.24.

In summer, fawn home ranges were larger ($P \leq 0.01$) in maneuver ($n = 21$) than previous-maneuver ($n = 12$) areas in 2 of 3 analyses (50% HMT; $P = 0.20$). Fall maneuver ($n = 3$) and previous-maneuver area ($n = 7$) home ranges of fawns were similar ($P = 0.17$ – 0.82) in size (Table 3) as were annual home ranges in maneuver ($n = 4$) and previous-maneuver ($n = 6$) areas ($P = 0.59$ – 0.91). However, the statistical power of the 50% HMT summer, fall, and annual fawn analyses ranged between 0.10 and 0.40.

For bucks, seasonal home ranges were similar ($P > 0.59$) between maneuver and nonmaneuver areas during fall ($n = 7$) and nonfall ($n = 4$) (Table 4). The 50% HMT estimate of buck annual home ranges was larger ($P = 0.056$) under maneuver ($n = 8$) than nonmaneuver ($n = 7$) conditions. However, there was no difference among treatments for the convex polygon ($P = 0.95$) and 95% HMT ($P = 0.95$) estimators. The statistical power for the buck analyses, excluding the 50% HMT annual comparison, was 0.10.

Home Area Fidelity

More radiomarked does in maneuver areas (40%) than in nonmaneuver areas (12.5%) shifted location or use pattern of home areas between the premaneuver and maneuver periods ($P = 0.049$). During fall 1987, 1 of 4 does in maneuver areas ($P < 0.02$) and 0 of 4 does in control areas ($P > 0.30$) shifted home areas between the premaneuver and maneuver periods (Table 5). Similarly, 2 of 6 does in maneuver areas ($P < 0.005$) and 0 of 4 in control areas ($P > 0.15$) shifted home areas between premaneuver and maneuver periods during winter 1988 (Table 5). Both does that shifted use areas moved greater average distances between locations during the maneuver.

In summer 1986, 4 of 10 does in maneuver areas ($P < 0.1$) and 0 of 4 does in the control ($P > 0.2$) shifted home areas (Table 5). Of the 4 that shifted, the average distance moved during the maneuver compared to the premaneuver period was greater for 1 doe, similar for 2, and less for 1. However, during summer 1988, 2 of 4 does in control areas shifted home areas

Table 3. Mean (SE) seasonal and annual home range size of radiocollared fawn mule deer by training conditions on the Piñon Canyon Maneuver Site, Colorado, January 1986–September 1988.

Period	Area conditions	n	Convex polygon (km ²)	50% HMT (km ²)	95% HMT (km ²)
Summer	Maneuver	21	5.86 (0.94) A*	1.16 (0.24) A	11.42 (2.36) A
	Previous-maneuver	12	2.46 (0.55) B	0.73 (0.16) A	4.16 (1.37) B
Fall	Maneuver	3	5.79 (2.20) A	2.81 (1.08) A	7.76 (2.69) A
	Previous-maneuver	7	4.21 (0.59) A	1.03 (0.11) A	6.74 (1.02) A
Annual	Maneuver	4	7.63 (1.83) A	1.55 (0.60) A	11.02 (2.68) A
	Previous-maneuver	6	11.34 (4.19) A	1.57 (0.30) A	14.33 (5.53) A

* Means within the same column and season that share the same letter are not significantly different ($P > 0.1$) according to Wilcoxon Rank Sum test.

Table 4. Mean (SE) seasonal and annual home range size of radiocollared adult male mule deer by training conditions on the Piñon Canyon Maneuver Site, Colorado, January 1986–September 1988.

Period	Area conditions	n	Convex polygon (km ²)	50% HMT (km ²)	95% HMT (km ²)
Fall	Maneuver	3	11.34 (3.34) A ^a	1.43 (0.77) A	22.43 (7.59) A
	Nonmaneuver	4	18.56 (9.85) A	2.35 (0.93) A	43.43 (22.75) A
Non-fall (winter, spring)	Maneuver	3	6.46 (2.35)	2.10 (0.87)	8.33 (2.43)
	Nonmaneuver	1	2.04	0.56	1.98
Annual	Maneuver	8	28.89 (11.12) A	5.79 (1.19) A	47.87 (16.10) A
	Nonmaneuver	7	41.67 (18.72) A	3.36 (0.46) B	74.21 (36.03) A

^a Means within the same column and period that share the same letter are not significantly different ($P > 0.1$) according to Wilcoxon Rank Sum test.

($P < 0.04$) and 5 of 10 in the maneuver area shifted home areas ($P < 0.006$) (Table 5). The 2 control does that shifted home areas moved shorter average distances during the maneuver

period. Four of the 5 deer in maneuver areas that shifted home areas moved shorter distances and 1 moved similar distances during the maneuver. Although sample sizes during postma-

Table 5. Home area fidelity of radiocollared adult female mule deer by training conditions before and during maneuvers on the Piñon Canyon Maneuver Site, Colorado, as determined by MRPP^a analysis.

Area conditions	Doe no.	<i>P</i> -value ^b			
		Fall 1987	Winter 1988	Summer 1986	Summer 1988
Maneuver (treatment)	034			0.029 ^c	0.0009 ^c
	053			0.717	
	054			0.626	0.1001
	063			0.459	
	065				0.128
	073				0.00006 ^c
	093			0.050 ^d	
	113			0.241	
	123			0.091 ^c	
	152			0.791	0.0001 ^c
	153	0.112	0.325		
	163				0.165
	164	0.112	0.453		
	172				0.576
	194			0.007 ^c	
	241		0.474		
	243			0.773	0.005 ^c
	251		0.005 ^d		
	543	0.016 ^c	0.403		
	693	0.514	0.002 ^d		
Nonmaneuver (control)	893				0.671
	914				0.0004 ^c
	051	0.874	0.173		
	133	0.750	0.157	0.812	0.008 ^c
	141				0.431
	143			0.210	
	172			0.931	
	241				0.038 ^c
	693			0.420	0.521
	933	0.346	0.294		
	983	0.775	0.202		

^a Multi-response permutation procedures.

^b $P < 0.1$ denotes significant shift in use area between premaneuver and maneuver periods.

^c Home area sizes were similar between premaneuver and maneuver periods.

^d Home area size was greater during maneuver than premaneuver period.

^e Home area size was less during maneuver than premaneuver period.

neuver periods were too small for statistical testing, all does that moved from their home areas eventually returned to them.

DISCUSSION

Mule deer increased their home range size in response to military training activity on the PCMS. Thus, we rejected the hypothesis that there was no difference in home range size between deer in maneuver and nonmaneuver areas. Mean convex polygon home range size of radiocollared does was 4.6-fold and 3.1-fold greater in maneuver than in nonmaneuver areas during the non-summer and summer periods, respectively. The 50 and 95% HMT estimators also reflected this large difference in home range size between animals that were and were not exposed to training activity, indicating that deer responded not only by moving out of their normal home ranges during maneuvers, but by increasing their core home ranges within maneuver areas. Furthermore, does in areas exposed to previous, but not current maneuvers used larger areas than does in nonmaneuver areas. Thus, deer exposed to military training used larger areas for extended periods. Although we could not compare home ranges of fawns in training areas with nonmaneuver controls, fawns in active training areas during summer used larger home ranges than fawns in previously maneuvered, but not current maneuver areas. We did not observe significant differences in seasonal home ranges of bucks, however, as estimated by the 50% HMT estimator, bucks in maneuver sectors had significantly larger annual home ranges than those in nonmaneuver sectors. This difference may appear only with the 50% HMT home ranges because the other 2 estimators were influenced more by distant locations that occurred on excursions during the fall rut. Furthermore, although many of the buck and fawn analyses detected no difference among treatments, the tests exhibited low statistical power.

Direct harassment and habitat alteration may have affected deer movements during maneuvers. Harassment of deer in maneuver areas may have been unintentional and intentional. Occasionally, tactical vehicles actively pursued pronghorn across the prairie (T. P. Gerlach, U. S. Fish and Wildl. Serv., pers. commun.). Deer were exposed to battlefield simulations involving machine gun and cannon fire (no live am-

munition). Traffic during training included jeeps, trucks, armored personnel carriers, tanks, helicopters, and jet fighter overflights. Bivouacs and encampments provided longer-term occupation of specific sites. Extensive (≥ 3 ha) smoke screens and tear gas clouds also may have influenced deer movement. Although mock battles and offensive encounters were conducted on the prairie, the Army used pinyon-juniper/grassland interface extensively for bivouacs and encampments (Fig. 1). The pinyon-juniper and shrub vegetation types, which were primary deer habitat (Gerlach 1987), provided excellent camouflage for military vehicles.

Habitat alteration from training maneuvers (Shaw and Diersing 1990) also may have affected deer movements. Shaw and Diersing (1990) noted that pinyon-juniper and shrubby vegetation densities on the PCMS were significantly reduced by an average of 9% under maneuver conditions. Grass species composition exhibited a shift from perennial to annual vegetation and the percentage of bare ground increased on disturbed areas (Shaw and Diersing 1990). These changes to PCMS vegetation may at least in part explain the increased home range sizes for does in previous-maneuver areas, in that deer in previous-maneuver areas probably required a larger area to meet forage and cover requirements. Habitat alteration, in addition to direct harassment, may have contributed to the increase in home range sizes during maneuvers. In summary, deer in military training areas may have responded to (1) human harassment or activity, (2) alteration of security cover, and (3) alteration of the forage base.

During winter and fall maneuvers, some deer in maneuver and previous maneuver, but not control areas, exhibited significant shifts in their use areas. Not only did deer temporarily abandon areas, but during the 1988 winter maneuver 2 does moved much greater distances during the period of training activity. Shifts in and contraction of areas used during summer may have been related to the behavior of does with young fawns. Does with fawns were unable to move large distances to escape areas of training activity, so they occupied a limited area beyond their usual use area. No instances of radiocollared does abandoning their radiocollared fawns in response to military activity were observed. Why 2 does in nonmaneuver areas shifted between periods during summer 1988 is unclear. Either individual variation in responses or un-

detected instances of intense military activity may explain the extremes in deer movements.

Deer may have exhibited a greater response to the unexpected military activity on PCMS than if it were continuous and predictable in occurrence. Geist (1971a) observed that large mammals easily become accustomed to and less alarmed by predictable events that initially may evoke an intense response. Mountain sheep heart rates and behavior were most sensitive to the unexpected approach of humans (MacArthur *et al.* 1982). Similarly, deer may be more alarmed by tanks and other tactical vehicles not restricted to road travel than vehicles on roads. White-tailed deer in Wisconsin, responding to snowmobile traffic, increased the sizes of and shifted their home ranges (Dorrance *et al.* 1975) and increased their movements (Eckstein *et al.* 1979). However, white-tailed deer in Wisconsin and Maine (Richens and Lavigne 1978, Eckstein *et al.* 1979), and adult female mule deer in Colorado (Freddy *et al.* 1986) responded more to persons afoot than to snowmobiles. Disturbance to mule deer resulted in greater energy expenditure due to interrupted grazing and decreased food intake, disrupted bedding, and provoked running (Freddy *et al.* 1986).

In contrast to unpredictable stimuli, several forms of human activity generally occur with a more routine presence, and most evidence indicates that deer can habituate to this type of activity. For instance, mule deer exposed to mining activities exhibited movements similar to deer not exposed to these activities (Merrill *et al.* 1994). Espmark and Langvatn (1985) noted that newborn red deer calves rapidly habituated to repeated alarm stimuli. In addition, Irby *et al.* (1987) were unable to detect a response by mule deer to low-intensity oil and gas exploration and drilling activities in Montana, and Geist (1971b) noted that mule deer in Alberta, if protected from hunting and poaching, habituated to humans and housing developments.

The PCMS deer population increased movement and activity in response to unpredictable military activity. Geist (1971b) noted that single incidents of harassment may be insignificant, but the effects are cumulative and could lead to a decline in juvenile survival or aborted fetuses in females. Hobbs (1989) determined that extreme harassment of mule deer (2 disturbances/day, each causing animals to move 500 m) during a severe winter could double doe

mortality. Thomas (1982) found that pregnancy rates in caribou declined with decreasing levels of fat reserves and body weights. The increased movement exhibited by adult does exposed to maneuvers on PCMS could result in lower fecundity. Does subjected to military activity produced fawns during this study, but severe winter weather or summer drought coupled with increased military training could cause a decline in fecundity. Furthermore, overwinter survival of deer, particularly fawns, may decrease in response to human activity. Any disruption in fat deposition or conservation before or during winter may render fawns less able to thermoregulate in winter (Moen 1976). Moen (1978) noted the necessity of weight gain by deer in fall and believed that any disturbance interfering with foraging at this time may directly or indirectly increase mortality or decrease natality.

Destruction of habitat during military maneuvers is of particular concern. Suitable habitat is essential to deer irrespective of the predictability of human activity. Mackie and Pac (1980) expressed concern over the loss of deer habitat, particularly winter range, to subdivision housing developments in Montana. The importance of sufficient protective cover in reducing the effect of harassment has been demonstrated for deer (Richens and Lavigne 1978, Eckstein *et al.* 1979). If habitat destruction associated with maneuver rotations continues at the rate and magnitude of the late 1980s, pinyon-juniper forest and shrub cover, essential refuge for deer, probably will decline in maneuver areas. Shortgrass prairie requires 6–20 years to recover to even a short-lived perennial plant community following extensive denuding; recovery of pinyon-juniper woodland would take 75–150 years (Shaw and Diersing 1990). Continual use of the pinyon-juniper edge may push back the edge until much of the pinyon-juniper in maneuver areas is gone. PCMS management plans provide for 2 years of recovery time between maneuver rotations. Disturbed areas on PCMS largely depend on annual plant cover to maintain soil erosion rates at an acceptable level (Shaw and Diersing 1990). During periods of below-normal precipitation, loss of annual cover would expose soils to excessive erosion, particularly in steep terrain. However, the concurrent removal of cattle from PCMS and revegetation efforts with the initiation of military activity may counteract some of the negative effects of military activity

(Stephenson 1989). The recovery of vegetation from previous heavy cattle grazing, particularly in riparian areas (pers. observ.), probably has improved deer foraging and security habitat, especially in off-limits areas. Thus, the improvement of habitat in off-limits areas of PCMS may partially mitigate the loss of habitat in maneuver areas.

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Received 16 February 1995.

Accepted 20 May 1996.

Associate Editor: Hobbs.

EVALUATION OF A LINKED SEX HARVEST STRATEGY FOR CERVID POPULATIONS

BRUCE C. LUBOW, Department of Fishery and Wildlife Biology and Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523-1484, USA

GARY C. WHITE, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523-1474, USA

DAVID R. ANDERSON, Cooperative Fish and Wildlife Research Unit, National Biological Service, Fort Collins, CO 80523-1484, USA

Abstract: We evaluated the ability of the linked sex harvest strategy (LSHS) proposed by McCullough et al. (1990) to determine optimum harvest of cervid populations from harvest statistics alone. This strategy purports to optimize total harvest by adjusting female harvest in response to observed changes in male harvest, without knowing the population's size or vital parameters (age-specific survival and productivity), and without an explicit population model. To examine LSHS, we evaluated a series of population models spanning a range of assumptions and parameter values that encompass many cervid populations. Deterministic simulations and numerical optimization were used to examine the response of these models to LSHS. Both steady state and dynamic responses of harvest statistics proposed for detecting optimal yield were examined. Based on our analyses, we were unable to identify general conditions under which LSHS, as currently proposed, provides a sound basis for harvest management. Reliable information regarding a population's vital parameters and current size of each age-sex class remains the only sound basis for near-optimum big game management involving female harvests.

J. WILDL. MANAGE. 60(4):787–796

Key words: deer, harvest management, maximum sustained yield, optimization, population models, sex-selective harvest, simulation.

McCullough et al. (1990:7) propose a “black box paradigm” for big game harvest management. Under this paradigm, harvest decisions are based only on harvest information and do not depend on population estimates or knowledge of the population's vital parameters (survival and recruitment rates by age and sex class). Furthermore, decisions under this paradigm are guided by a set of generic criteria, rather than by an explicit population model. As an example of this paradigm, McCullough et al. (1990) proposed LSHS. The decision criteria proposed in LSHS, based only on harvest data (i.e., not on direct estimates of population size), presumably allow the manager to control harvest and obtain high yields while maintaining a margin of safety to avoid overexploitation. Given high costs of acquiring population estimates, difficulty of val-

uating population models, and frequent unavailability of reliable information, the black box paradigm is an appealing alternative to traditional big game management. In preliminary analyses, we modeled LSHS to compare and contrast it with alternate harvest strategies. However, we could not find any set of model conditions under which LSHS performed as advocated. Thus, we evaluated the assumptions and predictions of LSHS for an explanation of this failure.

The stated objective of LSHS is maximum sustained yield (MSY); however, for practicality, McCullough et al. (1990) place some additional restrictions on the harvest:

1. Males are harvested at a high constant rate (McCullough et al. 1990). This rate is select-