



1-31-2003

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Sweitzer, Richard Alan (2003) "Breeding movements and reproductive activities of porcupine in the Great Basin Desert," *Western North American Naturalist*. Vol. 63 : No. 1 , Article 1.
Available at: <https://scholarsarchive.byu.edu/wnan/vol63/iss1/1>

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BREEDING MOVEMENTS AND REPRODUCTIVE ACTIVITIES OF PORCUPINES IN THE GREAT BASIN DESERT

Richard Alan Sweitzer¹

ABSTRACT.—I assessed movements of North American porcupines (*Erethizon dorsatum*) in the Great Basin of northwestern Nevada in relation to reproductive activities during the late summer and fall periods of 1991 and 1992. Porcupines exhibit a mate-defense polygynous mating system and I hypothesized that (1) competitively dominant males would have larger home ranges than both subordinate males and adult females, and (2) variation in home range size among adult male porcupines would be positively correlated with reproductive success. Results indicated that dominant male porcupines ranged over larger areas (average 95% minimum convex polygon home range = 20.7 ha) than subordinate males (average 95% MCP home range = 2.9 ha) and adult females (average 95% MCP home range = 8.2 ha). Analyses of movements in relation to body size and energetic requirements revealed that home ranges of dominant male porcupines were larger than predicted based on body size (approximately 10.2 ha). Breeding period home ranges of dominant male porcupines encompassed portions of the home ranges of 3 to 10 adult females, and indices of reproductive success based on observations of mate-guarding behaviors suggested a strong positive relationship between home range sizes of male porcupines and mating success. Together these data suggested that larger home ranges among dominant males were related to increased mating opportunities and not increased metabolic requirements associated with larger male body sizes. In the study area, however, female porcupines congregated around small, patchily distributed riparian areas, and dominant males with relatively small home ranges encompassing riparian areas may have gained mating access to multiple females. Finally, analyses of overlap among core home ranges (60% MCP) of adult male and adult female porcupines suggested that both sexes maintained relatively exclusive core home range areas, with males exhibiting significantly less range overlap with other males (\bar{x} = 9.4%) than females with other females (\bar{x} = 27.1%). It is possible that the small, patchily distributed riparian areas in this desertlike area were such a limited resource that females were unable to maintain exclusive use of their home range areas.

Key words: *Erethizon dorsatum*, *Nevada*, *mating systems*, *reproductive behavior*.

Movements and spatial use of habitat are important for elucidating social behaviors and intraspecific and interspecific relations among animals (Gaulin and Fitzgerald 1988, Rachlow et al. 1998). In species with polygynous mating systems, variation in sizes of home ranges for males and females has been related to differences in body size and access to resources and mates (Cederlund and Sand 1994, Goodrich and Buskirk 1998). Home ranges of females must be large enough to include sufficient food for successful reproduction, whereas home ranges of males reflect a strategy to maximize access to females during the breeding period (Clutton-Brock 1989). In mate-defense polygynous systems males often course over large areas in search of females and gain access to them by dominance displays sometimes associated with direct male-male competition (Berger and Cunningham 1996). In contrast, the reproductive success of females in these systems is

influenced more by life history constraints and the energetics of producing surviving offspring (Emlen and Oring 1977, Robbins 1993, Berger and Cunningham 1994).

The North American porcupine (*Erethizon dorsatum*) is a medium-sized mammal with a range extending from northern Mexico into Alaska and Canada (Woods 1973). The mating system of this species has been characterized as mate-defense polygyny in which the reproductive success of males depends on the number of females they are able to monopolize during the late summer–early fall mating season, rather than the amount or quality of resources they control (Roze 1989, Sweitzer and Berger 1997). Reproductive success among female porcupines appears more related to life history constraints (litter size in this species is invariably one) and the availability of sufficient resources to meet energetic needs during gestation and lactation (Roze 1989, Sweitzer and

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Holcombe 1993). Associated with mating behaviors, male porcupines do not defend territories, and they range widely during the breeding period (mid-August to mid-November) in search of pre-estrous females (Roze 1989). Upon locating a pre-estrous female, several males may compete for guarding position, with the dominant male guarding the female for 1–3 days until copulation (Roze 1989). Competition for mate access among males often escalates from auditory threats and visual displays of incisors to battles in which rivals impale each other with quills and tear out patches of the other's hair and quills by biting (Dodge 1982, Sweitzer and Berger 1997). Thus, home ranges of dominant male porcupines may overlap the ranges of multiple females as well as the ranges of other males (Roze 1989). Among female porcupines home ranges also overlap, which is interesting because access to sufficient forage resources is expected to be a key component of female reproductive success. However, some evidence suggests that females maintain exclusive core areas within their home ranges (Roze 1989).

As part of a larger 5-year study of the population and behavioral ecology of porcupines, I studied the home range movements and reproductive behaviors of individual porcupines in the Granite Range of northwestern Nevada from April 1990 to November 1992. My objective was to test 3 hypotheses related to breeding period movements among mammals with mate-defense polygyny: (1) males should have larger home ranges than females during the breeding period, (2) home ranges among adult males will be related more to mate access than to metabolic demands, and (3) competitively dominant males will have larger home ranges than subordinate males, which will be positively correlated with indices of reproductive success. I also examined patterns of overlap among home ranges of males and females to assess whether female porcupines are more territorial than males associated with the importance of resource access for females in polygynous systems.

STUDY AREA

The research site was a 20-km² enclosed basin (Granite Basin; 40°44'N, 119°20'W) between 1520 and 1640 m elevation (Fig. 1). Granite Basin is characterized by sagebrush

steppe habitat interspersed with juniper trees (*Juniperus osteosperma*) and multiple rock outcroppings (Fig. 1). Within Granite Basin there are 3 small spring areas, which provide important riparian habitat for many vertebrates including porcupines. The riparian habitat around these springs, hereafter referred to as "groves," is a complex of buffalo-berry (*Shepardia argentea*), willow (*Salix* sp.), and a variety of other riparian shrubs and plants (Fig. 1). Porcupines in Granite Basin focused their activities around the 3 different groves, which provided forage, water, protective cover, and den sites. Rock outcroppings and juniper shrubland also were used for den sites, and grassland/shrubland habitats were frequented by porcupines during spring and early summer when emergent vegetation provided forage (Fig. 1). The 3 grove areas were spatially separated such that most individual porcupines included a single grove area within their home ranges. Movements of some females and several male porcupines encompassed more than 1 grove area.

MATERIALS AND METHODS

All porcupines in the Granite Basin were captured and individually marked upon initial observation; all resident adult males and females were known. Individual porcupines were located using dogs, a spotting telescope, night-vision equipment, radiotelemetry, and tracking when snowcover was present during systematic surveys of foraging areas and den sites. Additional details on surveys used to assess population sizes are presented elsewhere (Sweitzer 1996), but population size during the April to November period was estimated at 75 in 1991 and 46 in 1992. Animals were captured by ascending trees or approaching their positions in other habitats for immobilizations with a jab stick loaded with ketamine hydrochloride (dosage 10 mg · kg⁻¹) and xylazine hydrochloride (4 mg · kg⁻¹). Each animal was fitted with a numbered color ear tag (Allflex style C12334-8 [Dallas, TX], modified and attached with aluminum self-piercing domestic livestock ear tags [National Band and Tag Company, Newport, KY]), weighed, and measured for mid-sternal chest circumference, middorsal and mid-ventral body length from tip of nose to end of tail, and length of the left footpad. Ages were determined from body mass and body dimensions or known from birth (Sweitzer and Berger

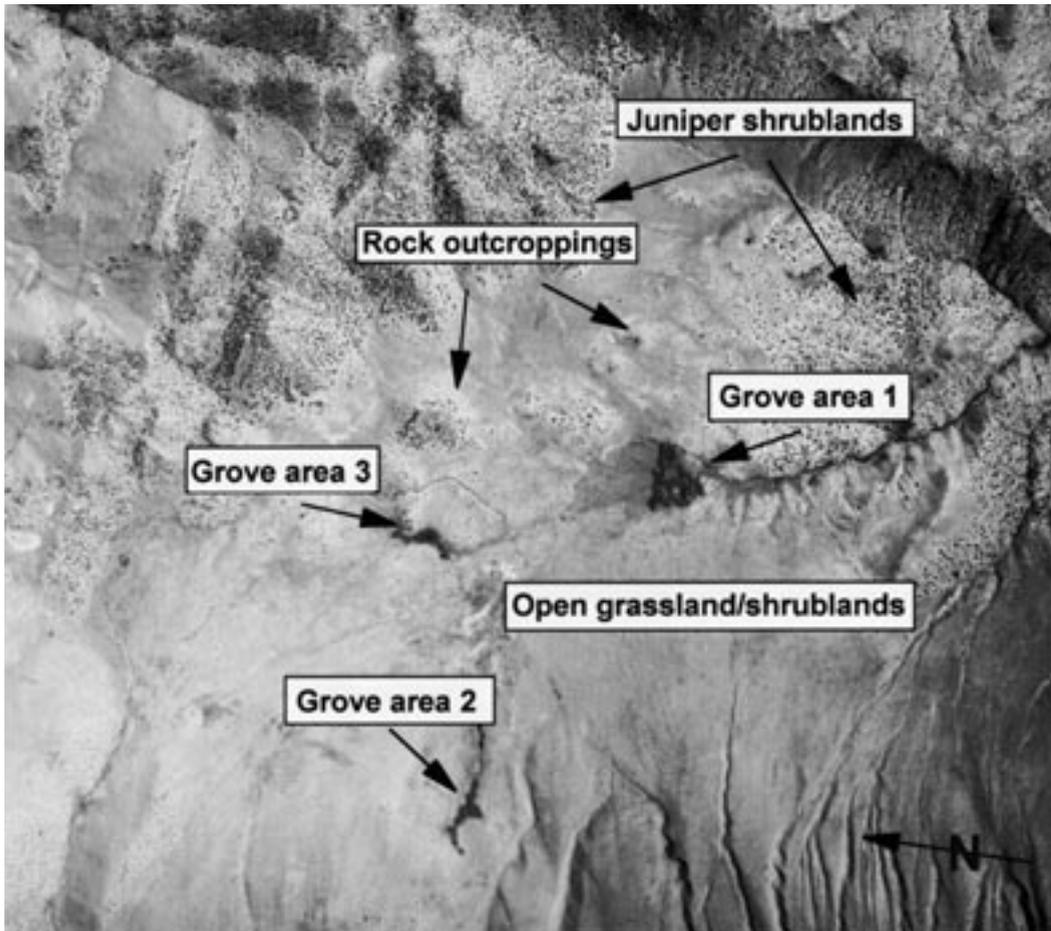


Fig. 1. Aerial photograph of Granite Basin study area showing different habitats used by porcupines including 3 small grove areas focused around permanent springs, several rock outcroppings, and juniper and sagebrush shrublands. Grove areas were important habitats for a variety of activities (forage, refuge from predators, den sites, mating activities, etc.); rock outcroppings were important for den sites; open grassland/shrublands were used for foraging during different periods of the year; and juniper shrubland habitats (interspersed with rock outcroppings) also provided den sites.

1992, 1993). Individuals were periodically recaptured to monitor growth and hormone levels in blood associated with reproduction (Sweitzer and Holcombe 1993). Forty-one different porcupines were fitted with radio-collars (AVM Instrument Company, Livermore, CA; Custom Electronics, Urbana, IL) during the study period (April 1991 to December 1993). Only adult-aged animals (≥ 18 months) were selected for monitoring by radiotelemetry, due to a research focus on different aspects of reproduction and mating behaviors. However, locations of other porcupines also were noted during the systematic surveys of the study area. Radio-collared porcupines were located by homing to positions. Upon visual contact, location information was

recorded and later mapped on a detailed drawing of the Granite Basin study site. Subsequently, Universal Transverse Mercator (UTM) coordinates were assigned to each position (accuracy estimated at ± 10 m), aided by an aerial photograph of the Granite Basin area, which was registered in a geographical information system (TNT Mips, MicroImages, Inc., Lincoln, NE). The aerial photograph was prepared by scanning the image and assigning UTM coordinates to multiple geographical landmarks obtained from a 7.5-minute United States Geographical Survey map of the area.

In this study I generally had fewer than 25 locations for each individual during the summer to fall period (15 June to 31 November)

encompassing the breeding season. Boulanger and White (1990) noted that minimum convex polygon (MCP) methods can provide reliable estimates of home range areas when number of measurements is limited. Therefore, I estimated 95% MCP home range areas for the porcupines monitored during this study using the computer program RANGES V (Kenward and Hodder 1996). Individual animals included in home range analyses were those for which ≥ 12 locations were available within the period from 15 June to 31 November 1992 and 1993. The "core" region of individual home ranges (area of intensive use including den sites and other resources necessary for survival) was defined as the MCP home range area which included 60% of an animal's positions. I selected the 60% MCP as the core home range based on examination of multi-range utilization plots produced by RANGES V (Kenward and Hodder 1996). As detailed by Kenward and Hodder (1996), home range utilization plots for multiple individuals may be used to identify the core region of home ranges for animals as the point at which variation in home range size tends to a minimum, which is the percentage of fixes that excludes most excursive activity. Significant autocorrelation can occur if an animal moves either less or more between sequential locations than between nonsequential locations, related to an individual's past experience and knowledge of resources within home ranges (Powell 1987). To avoid serial autocorrelation, consecutive locations were separated by at least 24 hours.

As part of behavioral monitoring of porcupines during the 1991 and 1992 breeding seasons, I noted mate-guarding episodes between male and female porcupines and whether males suffered foreign quill impalements or injuries (detailed by Sweitzer and Berger 1997). Guarding episodes were defined as close associations between male and female porcupines (distances of separation ≤ 5 m) for 1–3 days during the mating season. Guarding episodes in this species are often associated with vocalizations by females that attract other adult males, sometimes leading to direct male-male competition for guarding position (Roze 1989, Sweitzer and Berger 1997). During contests for guarding position, male combatants often suffer quill impalements and loss of patches of quills from bites (quill patch injuries). Thus, I used data on guarding associations, foreign quill impalements,

and quill patch injuries (noted when animals were periodically captured during breeding periods; Sweitzer and Berger 1997) to identify adult male porcupines that were reproductively active (observed in mate-guarding associations or quilled or injured) or not reproductively active (not observed in mate-guarding associations nor quilled or injured). Assuming that males that guarded females were relatively dominant compared to those that did not guard females, I compared the 95% MCP home ranges of these 2 classes of males to test the hypothesis that dominant males would have larger home ranges than subordinate males during the breeding period. I also assessed whether adult male porcupines had larger 95% MCP home ranges than adult females.

North American porcupines are sexually dimorphic in body size, with adult males in the study population averaging 35% larger than adult females during late summer (Sweitzer and Berger 1997). Thus, potentially larger home ranges among adult male porcupines may be a function of increased metabolic requirements related to body size. To test the hypothesis that home ranges of male porcupines are larger than home ranges of females due to mating behaviors and not simply because of larger male body sizes, I assessed whether observed sizes of home ranges for males were equivalent to those that would be predicted based on energetic requirements (Gehrt and Fritzell 1997, Goodrich and Buskirk 1998). Adult female porcupines raise offspring without the assistance of males, and female reproductive success is coupled with the availability of sufficient resources to produce surviving offspring. Therefore, I assumed that sizes of home ranges of females were set by metabolic demands (the area used by a female reflected that needed to satisfy energetic requirements in the Granite Basin area; Gehrt and Fritzell 1997), and I used the mean size of observed home ranges for females to calculate the predicted home range of males based on body size from the formula (Sandell 1989):

$$HR_{\text{male}} = \frac{HR_{\text{female}} \times \text{Mean body mass}_{\text{male}}^{0.75}}{\text{Mean body mass}_{\text{female}}^{0.75}}$$

Data on body masses for males and females used in this calculation were the mean body masses for radio-collared adult females and radio-collared adult males measured during

the late summer–early fall time periods of each year.

To assess the extent to which home range sizes among adult male porcupines may be related to reproductive success (e.g., do males with larger home ranges experience greater reproductive success?), I calculated index scores of male reproductive success based on (1) the numbers of adult females included within the 100% MCP ranges of adult male porcupines during the breeding seasons in 1992 and 1993 and (2) observations of mate-guarding associations (Table 2). It was possible that a few females that were transient within a male's range and within Granite Basin in general were not detected. However, because all resident or transient individuals that were observed were captured and marked and because survey efforts were intensive and systematic during the breeding period, the minimum number of females scored as present within an individual male's home range likely approached the total (but see Discussion for individual male R3). The total number of adult females (radio-collared and non-radio-collared females) that were within ranges of individual males was determined by mapping the locations of all females noted in the period from 1 September to 31 October (most active period of mating activities; Sweitzer and Holcombe 1993; unpublished data on serum testosterone levels) within the 100% MCP home range outlines of each male using the range overlap feature of RANGES V. Observations of mate-guarding associations then were used to assign point values representing the probability that an individual male mated with each female observed within his range. The reproductive success index score for each male was calculated as the sum of point values assigned for each female noted within the range of the male. Assignments of reproductive success point values were as follows: 1.0 if a male guarded a female for at least 2 days, 0.75 if a male guarded a female 1 day and no other males guarded her, 0.5 if a male guarded a female but other males also guarded her, 0.25 if an individual female was observed within a male's home range but was not guarded by the male or observed being guarded by other males, 0.125 if an individual female observed within a male's home range was not guarded by the male but 1 other male guarded her, and 0 if an individual female observed within a male's home range was not guarded

by the male but at least 2 other males guarded her (Table 2). A linear regression analysis was used to assess the relationship between reproductive success index scores and the 95% MCP home range sizes of adult male porcupines.

Because female mammals require access to sufficient resources to support energetic costs of gestation and lactation, female porcupines may maintain relatively more exclusive territories than male porcupines. To examine potential differences in home range overlap related to sex, I calculated overlap of 95% and 60% MCP home ranges among radio-collared porcupines using the range overlap analysis options in RANGES V. Ranges of pairs of animals were considered to overlap when at least 2% of an animal's range was within the range of another. Statistical analyses of overlapping home ranges were based on geometric mean overlaps (Minta 1992). For any 2 animals, a and b , the geometric mean overlap was calculated as the product of the ratios of overlap size to the size of the home ranges of the individuals (Minta 1992, 1993):

$$\text{Mean overlap} = \left(\frac{\text{Overlap area}}{\text{Home range a}} \times \frac{\text{Overlap area}}{\text{Home range b}} \right)^{0.5}$$

Home ranges of reproductively active males were compared to home ranges of non-active males, and both classes of males were compared to females. All comparisons were made using Mann-Whitney U tests. I pooled predicted and observed home ranges for reproductively active males for each year because of small samples and used a paired t test to compare predicted and observed sizes of home ranges of males. Means are presented $\pm 1 s_{\bar{x}}$. All statistical analyses were completed with SYSTAT 8.0 (SPSS Inc., Chicago, IL).

RESULTS

Overlays of the 95% MCP home ranges of adult female porcupines and the composite 95% MCP ranges of adult males on an aerial photograph of the study area (Figs. 2, 3) illustrate the general pattern of porcupine movements in Granite Basin. All but 1 of 22 adult female porcupines monitored during the study occupied a portion of at least 1 grove area during the breeding season (Figs. 2, 3). The composite ranges of 4 and 6 adult male porcupines in 1991 and 1992, respectively, encompassed



Fig. 2. Plots of 95% minimum convex polygon home ranges for radio-collared adult female porcupines and a composite 95% MCP home range for radio-collared adult male porcupines in 1991. Home range outlines were overlaid on an aerial photograph of the Granite Basin study area to illustrate patterns of habitat use in relation to different habitat features (groves, rock outcroppings, juniper shrublands, and grassland/shrublands).

parts, or the entire ranges, of all 22 adult females. In general, the portions of female and male home ranges away from grove areas included den sites in rock outcroppings or juniper trees. Although all 3 grove areas were used by adult females in 1992, grove area 2 was not used by radio-collared adult females in 1991.

Home ranges of adult male and adult female porcupines in Granite Basin during the summer and fall periods of 1991 and 1992 averaged 15.3 ha and 8.2 ha, respectively (Table 1; Mann-Whitney U test = 135, $df = 1$, $P = 0.31$). Although all radio-collared adult females were reproductively active in one or both years, not

all adult male porcupines were reproductively active (Table 2). Three of the 10 radio-collared adult males were not detected guarding females or observed with quill impalements or injuries (Table 2). In relation to mating activities, reproductively active adult male porcupines ranged over larger areas than adult females (Table 1; Mann-Whitney U test = 125, $df = 1$, $P = 0.014$), whereas adult males not involved in mating activities had smaller home ranges than adult females (Mann-Whitney U test = 10, $df = 1$, $P = 0.054$) and reproductively active adult males (Mann-Whitney U test = 19.0, $df = 1$, $P = 0.053$).

Large home ranges observed among repro-

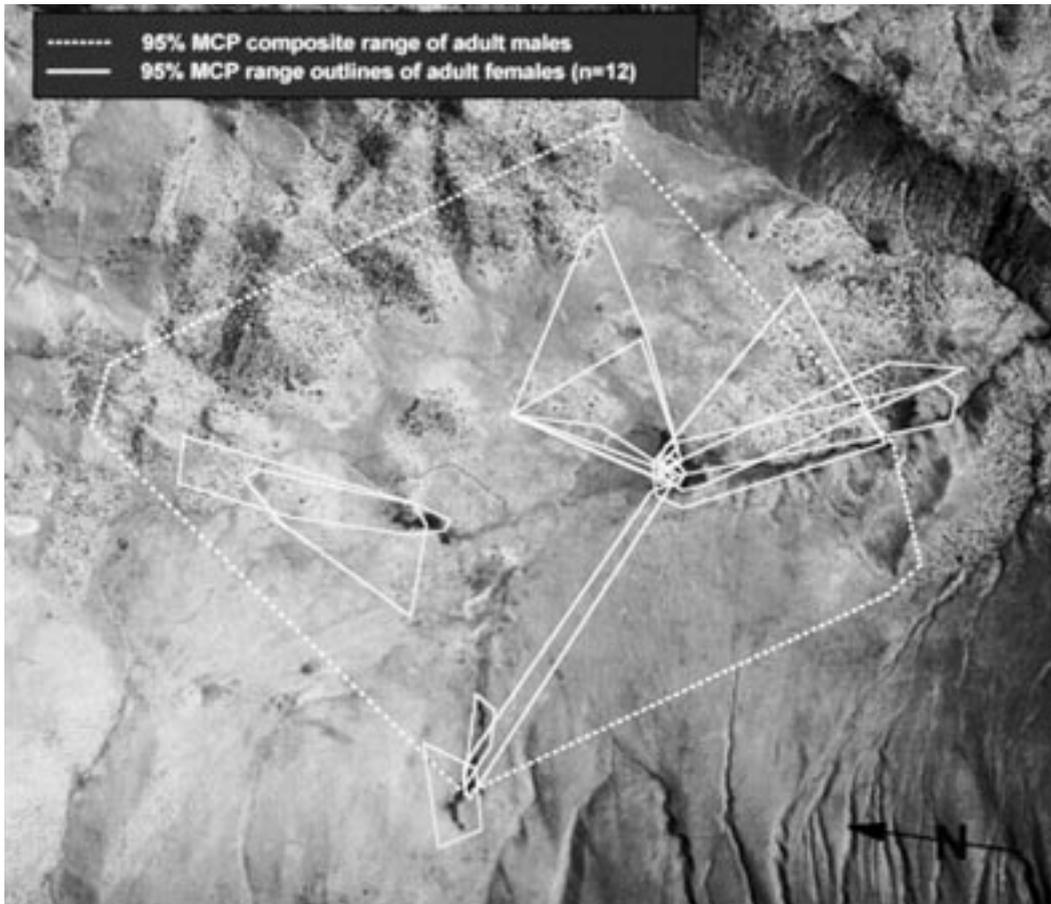


Fig. 3. Plots of 95% minimum convex polygon home ranges for radio-collared adult female porcupines and a composite 95% MCP home range for radio-collared adult male porcupines in 1992. Home range outlines were overlaid on an aerial photograph of the Granite Basin study area to illustrate patterns of habitat use in relation to different habitat features (groves, rock outcroppings, juniper shrublands, and grassland/shrublands).

ductively active male porcupines were not linked to body size. The average 95% MCP home range size of reproductively active male porcupines was 2 times greater than predicted (10.2 ha) based on body size ($t = 2.77$, $df = 6$, $P = 0.032$). In contrast, the average 95% MCP home range size of 3 adult males that were not active during the breeding season ($\bar{x} = 2.9 \pm 2.0$ ha) was over 3 times smaller than predicted (9.0 ha) based on body size ($t = -3.14$, $df = 2$, $P = 0.09$). However, sizes of core home ranges of adult male porcupines were similar to predicted based on body size (Table 1; $t = 0.37$, $df = 9$, $P = 0.72$). The 60% MCP home ranges of males were pooled in this analysis because they were similar for both classes of

males.

Although reproductively active adult male porcupines ranged over larger areas than non-reproductively active adult males (Fig. 2, 3), they apparently did not encompass more adult females within their larger ranges. Reproductively active adult males overlapped the ranges of 7.4 ± 1.1 adult females, whereas non-reproductively active males overlapped the ranges of 5.7 ± 0.7 (Table 2; Mann-Whitney U test = 14.5, $df = 1$, $P = 0.35$). Nevertheless, males with large home ranges were successful in mating activities because their larger home range sizes were positively related to indices of reproductive success based on mate-guarding associations ($\text{adj } R^2 = 0.77$, $df = 1,8$, $P = 0.01$;

TABLE 1. Summary of home range data for porcupines in Granite Basin in summer and fall (June 15 to November 31) 1991 and 1992.

Group	N	95% MCP range (ha)		60% MCP range (ha)	
		Observed	Predicted ^a	Observed	Predicted
Adult males	10	15.3 ± 3.8	9.9 ± 0.3	3.3 ± 2.0	2.6 ± 0.1
active ^b	7	20.7 ± 3.7	10.2 ± 0.2	4.6 ± 2.8	2.7 ± 0.1
inactive	3	2.9 ± 2.0	9.0 ± 0.4	0.3 ± 0.1	2.4 ± 0.1
Adult females	22	8.2 ± 1.5		2.1 ± 0.6	

^aPredicted home range based on body size.

^bReproductively active adult males were observed guarding females during mating seasons and were noted with quill impalements or injuries. Reproductively inactive adult males were not observed guarding females or noted to have quill impalements or injuries.

TABLE 2. Summary of reproductive activities of adult male porcupines in Granite Basin during the breeding seasons in 1991 and 1992.

ID	Year	Adult females within 100% MCP range	Number females observed guarding	Reproductive success index scores	95% MCP home range (ha)
W18	1991	5	0	0	0.8
O13	1991	5	0	0	0.9
B1	1991	10	3	3.5	24.9
W3	1991	8	3	3.125	28.7
O67	1992	10	1	2.0	21.1
W5	1992	7	2	2.25	21.4
W3 ^a	1992	4	3	2.75	0.9
B2	1992	10	3	3.375	30.3
Y9	1992	7	0	0	6.9
R3	1992	3	3	2.25	17.4

^aIdentified as a statistical outlier; see text.

Table 2). The regression analysis identified a single adult male porcupine as an outlier (W3 in 1992); this male had a small 95% MCP home range but a relatively high score for reproductive success (Table 2). When this male was removed from the analysis, the fit of the regression model describing the relation between indices to reproductive success and home range size was significantly improved ($y = -0.274 + 0.125x$; $\text{adj } R^2 = 0.93$, $\text{df} = 1, 7$, $P = 0.0001$).

Data on home range overlaps during the breeding season suggested that adult female porcupines in Granite Basin maintained less exclusive territories than adult males. As illustrated graphically in Figures 2 and 3, the 95% MCP home ranges of adult female porcupines overlapped most significantly (average female-female 95% MCP range overlap = $20.4 \pm 3\%$) in and around grove areas. In contrast, average 95% MCP home range overlap among adult males was only $10.6 \pm 4.7\%$, which suggested a trend for less overlap of 95% MCP ranges among adult male than among adult female porcupines (Mann-Whitney U test =

120, $\text{df} = 1$, $P = 0.10$). Similarly, the 60% MCP core home range overlap was higher among adult females ($\bar{x} = 27.1 \pm 3.6\%$;) than among adult males ($\bar{x} = 9.4 \pm 2.8\%$; Mann-Whitney U test = 22, $\text{df} = 1$, $P = 0.008$).

DISCUSSION

Previous research on this population indicated that large, dominant male porcupines that guarded females suffered fewer quill impalements and injuries than subordinate males, providing a mechanism for the evolution of sexual size dimorphism in this species (Sweitzer and Berger 1997). This study extends our understanding of mating behavior in porcupines by revealing that dominant adult male porcupines ranged over larger areas than subordinate adult males and adult females, independent of greater metabolic needs related to larger body size (Table 1). This was important because the breeding period movements of dominant males overlapped the home ranges of 3 to 10 adult females, potentially resulting

in greater reproductive success among dominant males compared to subordinate males (Table 2). Roze (1989) noted a similar association between relatively large male porcupines and reproductive success. Although my data on indices of reproductive success support a positive relationship between home range size and reproductive success in porcupines, mating access to receptive females by males is gained primarily by dominance during male-male competition (Sweitzer and Berger 1997) and not solely by inclusion of females within a home range. For example, 3 subordinate adult males in this study moved over areas that overlapped with 5 to 7 different females, but behavioral data suggested they were unsuccessful at gaining access to any of those females during the mating season (Table 2).

Dominant males with large home ranges in Granite Basin appeared to experience relatively high reproductive success, but results from 2 of these males merit further discussion. One of these males (R3) had a range which overlapped with at least 3 adult females during the mating season. However, a significant portion of this animal's range extended into a region of Granite Basin that was not a focal area of research (northeastern area of Granite Basin; Fig 1). Although I occasionally surveyed the northeastern area of Granite Basin for porcupines during winter when snow conditions facilitated locating animals, I had little information on porcupines in this area. It is likely that the range of male R3 overlapped the ranges of several females unknown to the study, and his reproductive success index score was probably underestimated. The other male (W3) was tracked in both 1991 and 1992 (Table 2). In 1992 the range of male W3 was much smaller than in 1991, but his estimated reproductive success index score was relatively high in both years (Table 2). In 1991 the home range of male W3 encompassed portions of 2 of 3 grove areas in Granite Basin (Fig. 2), whereas in 1992 his range was focused around 1 grove area (Fig. 3). The relatively small grove area encompassed by the range of male W3 in 1992 was used by at least 4 different females, and he apparently had sole access to all of these females because I detected no other adult males in the area in 1992. Thus, by focusing his activities around a single small grove area in 1992, male W3 was able to gain mating access to multiple females and avoid the energetic cost of moving over a

larger area in search of mates.

Data on home range overlaps suggested that female porcupines in Granite Basin were less territorial than males, even though females have higher resource requirements for reproduction associated with gestation and lactation. Overlap of both 95% MCP and 60% MCP home ranges with other individuals of the same sex was less for adult male than adult female porcupines. In a study of porcupines in the deciduous forests of northeastern North America, Roze (1989) found that the non-winter core home ranges of females overlapped very little with other females, which he interpreted as due to agonistic behavior and competition among unrelated females for resources required for successful reproduction (natal dispersal is female-biased in this species; Roze 1989, Sweitzer and Berger 1998). Roze (1989) further noted that the non-winter ranges of males overlapped more than those of females, even though some males appeared to avoid each other. In our Granite Basin study site several small grove areas provide critically important habitat for porcupines (Figs. 2, 3). Both male and female porcupines congregated around these grove areas, where they foraged, denned, engaged in mating activities, and sought refuge from predators (Sweitzer 1996). It is possible that the patchily distributed grove habitats around springs in this desert environment are such a limited resource that females were unable to maintain exclusive use of even small core home ranges. Males, on the other hand, may have been able to maintain relatively exclusive home range areas associated with their large body sizes and dominance.

ACKNOWLEDGMENTS

This field portion of this study was supported by grants from Sigma Xi, the American Society of Mammalogists, the Theodore Roosevelt Fund of the American Museum of Natural History, Molly Knudtsen, and the Department of Environmental and Resource Sciences of the University of Nevada, Reno, through J. Berger. Thanks to those organizations and individuals for their support. C. Sorenson was instrumental in helping to compile data for analyses. V. Velez, A. Hodgson, and R. Loggins provided technical assistance. Thanks to Uldis Roze for comments that improved the manuscript.

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Received 17 July 2001
Accepted 24 April 2002