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Biological Conservation 104 (2002) 251–263

BIOLOGICAL
CONSERVATION

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Bighorn sheep habitat use and selection near an urban environment

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Received 27 February 2001; received in revised form 31 July 2001; accepted 31 July 2001

Abstract

To further understand the impact of urban development on wildlife populations, we examined habitat use and selection by female bighorn sheep *Ovis canadensis* in two endangered subpopulations near a metropolitan area in southern California. One subpopulation, which had previously been found to have low reproductive success, selected urban environments while the other did not use urban areas. In the subpopulation that used urban areas, females had smaller core activity areas and selected lower elevations and gentler slopes. These females used urban sources of water but a clear relationship between levels of urban use and periods of increased water need was not evident. Diet quality was higher among females that selected urban areas, and this increase was correlated with the level of urban use. Thus, optimal foraging behavior may have contributed to the selection of urban areas. Urban use was lowest during peak months of parturition, suggesting that reproductive strategies may also have influenced temporal patterns of urban use. Although urban areas provided bighorn sheep with forage and water resources, the use of these areas may have substantial costs. For example, females using urban areas had internal parasites that were not found elsewhere in the Peninsular Ranges. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Bighorn sheep; Habitat use; Habitat selection; *Ovis canadensis*; Urban

1. Introduction

Throughout the world, urban development is progressing at a rapid pace and an increasing number of wildlife populations are living within or at the edge of urban areas. Many urban wildlife studies have focused on the problem of wildlife–human conflicts (e.g. Brush and Ehrenfeld, 1991; Butfiloski et al., 1997), or assessed public attitude towards urban wildlife (e.g. Stout et al., 1997). Other studies have described the habitat use of urban-dwelling wildlife (e.g. Jodice and Humphrey, 1992; Ticer et al., 2001), or promoted urban environments as alternative wildlife habitat (e.g. Terman, 1997). There remains, however, a lack of information on how the use of urban areas impacts the behavior and ecology of wildlife. For most species, especially large mammals, urban development is equivalent to habitat loss and results immediately in altered ranging patterns, but animals that continue to use developed areas are also likely to exhibit changes in foraging and habitat selection behaviors. In some cases, such as in some populations of habituated North American elk *Cervus elaphus*, individuals that use urban areas may have increased fitness (Thompson and Henderson, 1998). However, altered foraging and habitat use behaviors may also have negative impacts on the long-term viability of populations or species, and may have important implications for the conservation of endangered species and biodiversity (Murphy, 1988). The goal of our study was to examine the habitat use and selection of a subpopulation of an endangered ungulate that regularly uses urban areas, and compare this with the behavior of a neighboring subpopulation that does not use urban areas.

Bighorn sheep in the Peninsular Ranges of the United States have been protected under California state law since 1971 and have been federally listed as an endangered population since 1998 (US Fish and Wildlife Service,

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PII: S0006-3207(01)00171-9

2000). Within these ranges, urban development has progressed rapidly along the northern and eastern slopes of the Santa Rosa Mountains, with many developments located within bighorn sheep habitat. One subpopulation of bighorn sheep, which lives close to urban areas northwest (NW) of Highway 74 (the "NW subpopulation"), has not grown in size although it was augmented with a total of 60 (28 male, 32 female) captive-reared animals between 1985 and 1994 (Ostermann et al., 2001). Low lamb recruitment has been documented in this subpopulation since the late 1970s (DeForge and Scott, 1982; DeForge et al., 1982; Wehausen et al., 1987; Ostermann et al., 2001) and females in this area exhibited the lowest lamb recruitment in a comparative study of reproduction among four of the eight subpopulations in the Peninsular Ranges during 1993–1996 (Rubin et al., 2000). Bighorn sheep in the NW subpopulation frequently feed and rest in urban areas, a behavior that has rarely been observed elsewhere in the Peninsular Ranges. The first objective of our study was to compare the diet and patterns of spatial habitat use by females in this subpopulation with those of females that live nearby on the southeast (SE) side of Highway 74 (the "SE subpopulation"). Bighorn sheep in the SE subpopulation live in an area of lower human impact and were never observed feeding in urban areas. In addition, females in the SE subpopulation exhibited high lamb recruitment relative to the NW subpopulation (Rubin et al., 2000). We compared diet by assessing diet quality, as indexed by percent fecal nitrogen (%FN), and the proportion of non-native plants in the diet of each subpopulation. Patterns of habitat use were compared by examining home range and core activity areas, group size, distance to water, habitat selection (slope and elevation), and use of urban areas.

Because habitat use may be influenced by the relative costs and benefits of obtaining resources and avoiding predation and disease (Milinski, 1988; Andersen and Skorping, 1991), our second objective was to explore potential costs and benefits associated with the use of urban areas. We examined whether females moved into urban areas and consumed non-native vegetation to compensate for seasonal declines in the quality of native vegetation, as predicted by optimal foraging theory (MacArthur and Pianka, 1966). Similarly, we examined whether distance to water was related to climate conditions in each subpopulation, and whether use of urban areas was related to increased periods of water need. We also tested the hypothesis that animals that feed in urban areas use gentler slopes, thereby possibly increasing the risk of predation to themselves and their lambs. During our study, some of the animals in the NW subpopulation were observed with poor body condition and diarrhea. Therefore, we also compared the prevalence of internal parasites in the two study groups.

2. Methods

2.1. Study area

Our study area was located in the Peninsular Ranges, which extend from southern California into Baja California, Mexico (Sharp, 1994; Fig. 1). The United States portion of this mountain province is located in the Colorado Desert subdivision of the Sonoran Desert (Jaeger, 1957). Bighorn sheep inhabit the eastern slopes of the Peninsular Ranges, and typically are found below approximately 1400 m elevation (Jorgensen and Turner, 1975). At least eight subpopulations, or ewe groups, currently inhabit the United States Peninsular Ranges (Rubin et al., 1998), and our study focused on two neighboring subpopulations in the Santa Rosa Mountains (33°38′ N, 116°23′ W). The NW subpopulation was found on the NW side of Highway 74 and was comprised of approximately 30 adults in 1994, while the SE subpopulation, comprised of approximately 90 adults in 1994, inhabited the area SE of that highway (DeForge et al., 1995).

On the eastern slopes of the Santa Rosa Mountains, vegetation associations are coniferous forest, consisting primarily of ponderosa pine *Pinus ponderosa*, Jeffrey pine *Pinus jeffreyi*, coulter pine *Pinus coulteri*, and white fir *Abies concolor* above approximately 1800 m, chaparral above approximately 1500 m, and pinyon pine *Pinus monophylla*-juniper *Juniperus californica* above approximately 1200 m. Lower elevations are dominated by agave *Agave deserti*, ocotillo *Fouquieria splendens*, cholla *Opuntia* spp., palo verde *Cercidium floridum*, creosote *Larrea tridentata*, and palo verde-mesquite *Prosopis* spp. associations (Ryan, 1968). Annual rainfall was variable between 1990 and 1997, with maxima of 50 to 2256 mm and a mean of 457 mm (NOAA, 1990–1997). Rainfall exhibited a bimodal pattern with the majority occurring in the winter months and the remainder occurring in late summer. Maximum temperature exceeded 40 °C every summer, while winters were mild, with temperatures rarely approaching freezing (M. Fisher, unpublished data, University of California, Philip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA).

2.2. Data collection and analysis

We captured female bighorn sheep in the SE subpopulation in autumn 1993 via netgun from a helicopter (Jessup et al., 1988), and fitted each animal with a radiocollar (Telonics, Inc. Mesa, AZ) and identifying eartag(s). Bighorn sheep in the NW subpopulation had been radiocollared as part of ongoing studies by the California Department of Fish and Game and the Bighorn Institute (Palm Desert, CA). We focused our study on females because bighorn sheep are polygynous, females form the basic unit of bighorn sheep social structure, and female bighorn sheep exhibit a high degree of philopatry (Geist, 1971). From March 1994 through December 1995, we attempted to locate and observe every radiocollared female once monthly at about 30-day intervals. During 1996 and 1997 we located animals less frequently. We assumed that recorded locations of individual animals were independent because animals were capable of crossing the entire study area in 1–2 days. At each observation, we recorded group size and composition, and marked the location of the group on a 7.5 min topographical map. Females were often observed more than once per month, but home range and habitat use analyses included only locations obtained when we were seeking a specific animal (at approximately 30-day intervals). This reduced the likelihood of bias in our results due to opportunistic observations made in areas we frequently visited. We also used this dataset for our examination of group size, to reduce any bias towards large groups which may be easier to detect opportunistically. We compared group sizes of the two subpopulations using Mann–Whitney *U*-tests (Sokal and Rohlf, 1995).

Home range areas were estimated by the adaptive kernel (Worton, 1989) and minimum convex polygon (Mohr, 1947) methods, using the program CALHOME (Kie et al., 1994). We generated 95 and 50% utilization distributions to represent home range and core activity areas, respectively. For the adaptive kernel analysis we set the grid size at 50×50 cells, and allowed the program to choose an optimum bandwidth (or smoothing parameter; Worton, 1989). We then repeated the analysis using 80 and 90% of this optimum bandwidth. We used the bandwidth that resulted in the smallest least-squares cross-validation score (Worton, 1989; Kie et al., 1994) to determine home range and core activity areas, unless this resulted in the utilization distributions breaking into more than two polygons. We used Mann–Whitney *U*-tests to test for differences in the median sizes of home range and core activity areas of the two subpopulations. We generated home range and core activity areas only for females with $\geqslant 18$ locations.

For our habitat selection analyses we defined the study area for each subpopulation by two methods and conducted our analyses twice, because the method of delineating study areas could have influenced our results and conclusions. We first delineated the study area as the area encompassed by the composite 100% minimum convex polygon home range of each subpopulation (including observations of uncollared females and males). Our second method of delineating the study area was to approximate the habitat available to bighorn sheep in both subpopulations. For the western and eastern boundaries, we used the western boundary of critical habitat for bighorn sheep in the Peninsular Ranges (Federal Register, 2001), and the edge of inaccessible urban areas, respectively. To delineate the southern and northern study boundaries, we connected

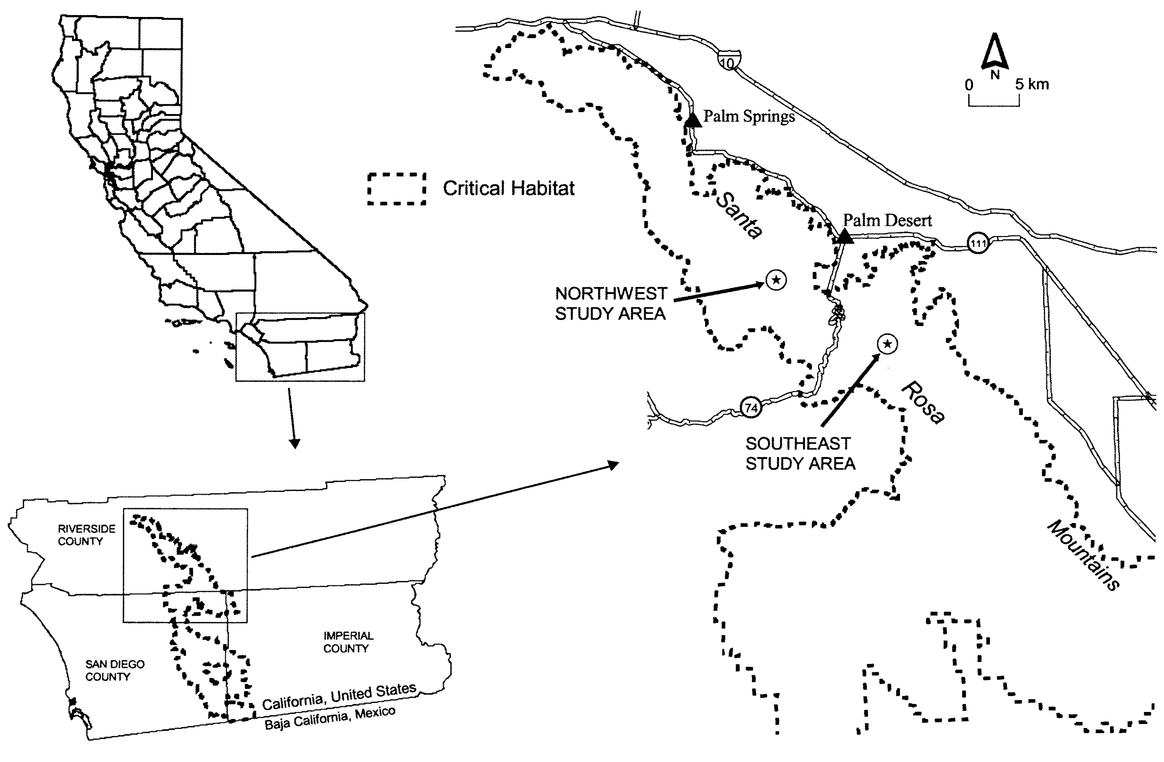

Fig. 1. Location of northwest (NW) and southeast (SE) study areas. Dashed line indicates boundary of critical habitat for bighorn sheep in the Peninsular Ranges, California (Federal Register, 2001).

the eastern and western boundaries with the shortest possible straight line that intercepted the northernmost and southernmost observed locations of radiocollared females in our study. We excluded areas inaccessible to bighorn sheep because of fences, walls, or major roads, and used Highway 74 as the division between subpopulations because no females were observed to cross this road during our study (Rubin et al., 1998). We delineated urban areas within the study areas by walking the urban interface and recording the path via a Global Positioning System. Known perennial sources of water were mapped and categorized as natural or man-made. Because an abundance of man-made water sources was available within urban areas (in the form of swimming pools, birdbaths, irrigation systems, etc.), we considered each of the urban areas to represent one large (man-made) water source.

We generated 1000 random points within each of the four study area polygons, and used these to estimate the relative availability of each habitat category (slope and elevation classes and urban areas; Marcum and Loftsgaarden, 1980). For each random location and for each bighorn sheep location, we calculated percent slope and elevation (meters) for the 30×30 m cell that contained the location and for each of the eight cells surrounding this cell. We generated these values with ArcView 3.2 and Spatial Analyst Extension 2.0 (Environmental Systems Research Institute, Inc., Redlands, CA). We used the mean value of the nine cells for our analyses to account for potential error in mapping accuracy. Slope was then assigned to one of nine classes: 0–20, 21–40, 41–60, 61–80, 81–100, 101–140, 141–180, 181–220, and $>220\%$ slope. Elevation was divided into eight classes: 1–200, 201–400, 401–600, 601–800, 801–1000, 1001–1200, 1201–1400, and >1400 m. We compared habitat use and availability using the Chi-square goodness-of-fit test (Neu et al., 1974; Byers et al., 1984), and applied Yates' correction when only two categories were present (Fowler et al., 1998). Bonferroni confidence intervals (95%) were generated following Byers et al. (1984). For each bighorn sheep location, we also determined the minimum distance to water (natural and man-made) and, for locations in the NW subpopulation, the distance to urban areas and whether the location was within or outside of an urban area.

We examined habitat selection by the two subpopulations for the entire study period using the habitat classes listed earlier, and then conducted additional evaluations for individual seasons. Season delineations were: February–April (peak birthing months; Rubin et al., 2000), May–July, August–October (fall rut months), and November–January. Because of sample size limitations, we collapsed our slope and elevation classes to three classes (1–100, 101–180, and $>180\%$) and two classes (0–400, and $\geqslant 401$ m), respectively, for the seasonal analyses.

Diet quality potentially plays an important role in determining habitat use patterns of bighorn sheep. To examine this potential influence, we used percent fecal nitrogen (%FN) as an index of diet quality (Leslie and Starkey, 1985). From October 1994 through September 1995, we attempted to collect a monthly fecal sample from each radiocollared female. Samples were analyzed for %FN using Kjeldahl procedures (Association of Official Analytical Chemists, 1984), at Washington State University's Habitat Lab (Pullman, WA). We used Mann–Whitney tests to compare %FN values between the two subpopulations. To evaluate the proportion of diet comprised of non-native plants, fecal samples collected during each season (represented by samples collected in December, March, June, and September) also were analyzed microhistologically (Sparks and Malecheck, 1968; Todd and Hansen, 1973) at the Range Analysis Laboratory (University of Arizona, Tucson). The botanical composition of each sample was estimated by reading 20 fields from each of three slides. Native plants were identified at least to the genus level, using a list of plants native to our study area (Zabriskie, 1979). Non-native plants were defined as those not known to occur naturally in the study area, and we determined the proportion of each sample composed of non-native plants.

To test for relationships between nutritional quality of native plants and the temporal pattern of urban use or consumption of non-native plants, we used the annual mean %FN value in the SE subpopulation to delineate periods of above- and below-average %FN. We assumed that the nutritional quality of native plants was similar in the two subpopulations since they were <10 km apart. We used Mann–Whitney tests to compare the percentage of the NW subpopulation's diet composed of non-native plants during periods of below- and above-average %FN. We used Spearman correlation analyses (Sokal and Rohlf, 1995) to test for relationships between monthly %FN values and the monthly proportion of locations occurring within urban areas, to test whether a nutritional advantage was gained by using urban areas. Similarly, we used Spearman correlation analyses to assess whether urban use was related to climate variables or periods of increased water needs (as indexed by distance to water from female locations in the SE subpopulation). We tested for relationships between monthly mean minimum distance to water, monthly mean high temperature and total precipitation (data collected at the Phillip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA), and the monthly proportion of NW locations occurring within urban areas. For those correlation analyses, we used only months for which we had $\geqslant 10$ observations.

In the summers of 1996 and 1997, and in the winter of 1997, we examined fecal samples from individually identified females in the SE subpopulation ($n=5$, 8, and 11, respectively) and in the NW subpopulation ($n=11$, 8, and 8, respectively) for parasite eggs using the McMaster technique (Soulsby, 1965). In the winter of 1997, we also collected and examined fecal samples from individually identified females outside of our study area. These samples came from distinct subpopulations (Rubin et al., 1998) in Coyote Canyon ($n=7$), the San Ysidro Mountains ($n=10$), and the Vallecito Mountains ($n=9$) in the southern portion of the Peninsular Ranges.

3. Results

Between March 1994 and December 1997, we recorded 449 ($n=13$ females) and 849 ($n=27$ females) observations in the SE and NW subpopulations, respectively. When we eliminated opportunistic sightings, the dataset was reduced to 238 ($n=13$ females) and 314 ($n=26$ females) observations in the SE and NW subpopulations, respectively. The maximum percentage of the total locations contributed by an individual female was 11% in the SE subpopulation and 8% in the NW subpopulation.

Group size was significantly larger (Mann–Whitney test, $P=0.001$) in the SE subpopulation (median = 6, range = 1–23) than in the NW subpopulation (median = 4, range = 1–21). Group size was larger in the SE subpopulation during every season ($P \leqslant 0.041$) except during August–October ($P=0.783$), when mean group size in the NW subpopulation was largest (Fig. 2a). Within the NW subpopulation, group sizes during August–October were significantly larger than in February–April ($P=0.022$) and, although they tended to be larger than group sizes in May–July and in November–January, these differences were marginally non-significant ($P=0.059$ and $P=0.056$, respectively; Fig. 2a). In the SE subpopulation, group size did not differ significantly among seasons. Home range sizes (95% utilization distributions) did not differ between SE and NW females (Table 1), but core activity areas (50% utilization distributions) were significantly smaller ($P=0.002$ for adaptive kernel estimation, and $P=0.015$ for minimum convex polygon estimation) in the NW subpopulation, regardless of method used. For home range and core activity analyses, the mean number of locations per female was 21.6 ($n=10$ females) and 21.0 ($n=10$ females) in the SE and NW subpopulations, respectively.

Females in the SE subpopulation used slope classes steeper than 180% more than would be expected by chance, they used slope classes of 101–180% in proportion to availability, and they used low slope classes (0–100% slope) less than would be expected by chance (Table 2). These results were identical regardless of how we delineated the SE subpopulation study area.

Table 1
Mean home range (95% utilization distribution) and core activity (50% utilization distribution) areas of bighorn sheep females in two subpopulations in the Santa Rosa Mountains, Peninsular Ranges, California (1994–1997). Areas (in hectares) were estimated by the adaptive kernel (AK) and minimum convex polygon (MCP) methods

	Southeast subpopulation		Northwest subpopulation	
	Mean	S.D.	Mean	S.D.
95% AK	2392.340	1932.602	1446.690	570.529
50% AK[a]	526.540	433.739	159.075	89.797
95% MCP	1502.010	1562.198	827.860	307.742
50% MCP[b]	246.765	157.788	130.195	156.939

[a] Estimates for subpopulations are significantly different ($P<0.01$).

[b] Estimates for subpopulations are significantly different ($P<0.05$).

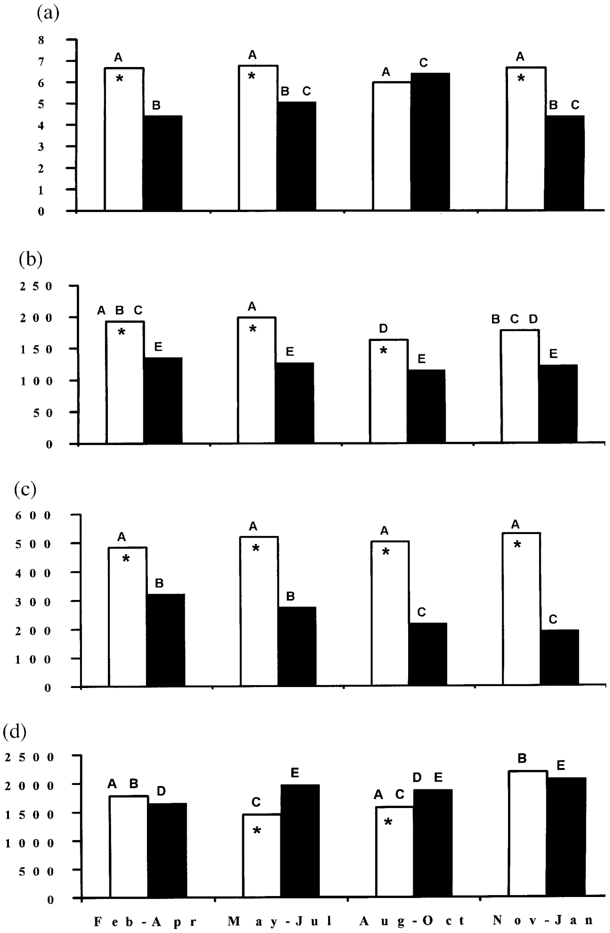

Fig. 2. Comparisons of group size and habitat use in two subpopulations of bighorn sheep in the Santa Rosa Mountains, Peninsular Ranges, California (1994–1997): (a) mean group size per season, (b) mean slope (%) of female locations per season, (c) mean elevation (meters) of female locations per season, (d) mean distance (meters) to natural water per season. Open bars denote the southeast (SE) subpopulation and closed bars denote the northwest (NW) subpopulation. Within each subpopulation, seasons sharing the same uppercase letter (A, B, C, etc.) were not significantly different from each other. (*) indicates a significant difference between the SE and NW subpopulations (Mann–Whitney test, $P<0.05$).

Although NW females also selected the steepest slopes (Table 2), they also selected the 141–180% slope class, which the SE females did not select. Females in the NW subpopulation were also not as consistent in avoiding low slope classes (0–100% slope). For example, the lowest slope class (0–20% slope) was used in proportion to availability, regardless of how we delineated the NW subpopulation study area.

When selection of slope was analyzed by season, SE females used steeper slopes than NW females did during every season except November–January (Fig. 2b). Females in the SE subpopulation consistently used slopes of $\leqslant 100\%$ less than expected by chance, and selected slopes $>180\%$, except in November–January, when this slope class was use in proportion to availability (Table 3). This result was not influenced by our method of habitat delineation. Females in the NW subpopulation also used low slopes (0–100%) less than expected by chance and selected habitat of steeper slope ($>180\%$) when the study area was delineated as our approximation of available habitat. However, when selection was evaluated within the composite home range of the subpopulation, NW females only exhibited this selection pattern during February–April. During the other three seasons these females used the low (0–100%) and medium (101–180%) slopes in proportion to availability, and only showed a preference for steeper habitat ($\geqslant 180\%$ slope) in May–July (Table 3).

The availability of slope classes differed significantly between the NW and SE study areas, with steeper habitat in the SE study area (Chi-square = 187.3, d.f. = 10, $P<0.001$ and Chi-square = 796.8, d.f. = 8, $P<0.001$ when availability was evaluated in the composite home range and in delineated habitat, respectively; Table 2). Urban areas were characterized by gentle slopes. Random locations in urban areas had mean slopes of 56.7 and 66.4% when the study area was delineated as the composite home range of the subpopulation and our approximation of available habitat, respectively (S.D. = 46.7 and 55.7, range = 8.2–208.4 and 9.22–170.9, respectively).

Females in the SE subpopulation used habitat of intermediate elevation (201–1000 m) either in proportion to availability or more than would be expected by

Table 2
Selection of slope and elevation by bighorn sheep females in two subpopulations in the Santa Rosa Mountains, Peninsular Ranges, California (1994–1997)

	Southeast subpopulation			Northwest subpopulation		
	Observed proportion of usage (95% C.I.)	Expected proportion of usage, study area = composite home range	Expected proportion of usage, study area = delineated habitat	Observed proportion of usage (95% C.I.)	Expected proportion of usage, study area = composite home range	Expected proportion of usage, study area = delineated habitat
Slope (%)						
0–20	0.004 (0–0.015)	0.029[a]	0.119[a]	0.048 (0.015–0.081)	0.031	0.036
21–40	0.008 (0–0.024)	0.050[a]	0.049[a]	0.083 (0.040–0.126)	0.087	0.149[a]
41–60	0.025 (0–0.053)	0.086[a]	0.083[a]	0.073 (0.032–0.114)	0.151[a]	0.165[a]
61–80	0.025 (0–0.053)	0.110[a]	0.097[a]	0.153 (0.097–0.209)	0.138	0.150
81–100	0.046 (0.008–0.084)	0.115[a]	0.102[a]	0.057 (0.021–0.093)	0.145[a]	0.136[a]
101–140	0.227 (0.152–0.302)	0.268	0.194	0.178 (0.119–0.237)	0.234	0.208
141–180	0.197 (0.126–0.268)	0.175	0.182	0.191 (0.130–0.252)	0.118[b]	0.110[b]
181–220	0.189 (0.119–0.259)	0.104[b]	0.100[b]	0.121 (0.070–0.172)	0.071	0.033[b]
>220	0.277 (0.197–0.357)	0.063[b]	0.074[b]	0.096 (0.050–0.142)	0.025[b]	0.013[b]
Elevation (m)						
0–200	0.029 (0–0.058)	0.074[a]	0.244[a]	0.487 (0.417–0.557)[c] 0.487 (0.410–0.564)[d]	0.107[b]	0.039[b]
201–400	0.303 (0.221–0.385)	0.213[b]	0.221	0.293 (0.229–0.357)[c] 0.293 (0.223–0.363)[d]	0.281	0.107[b]
401–600	0.353 (0.268–0.438)	0.165[b]	0.145[b]	0.213 (0.155–0.271)[c] 0.213 (0.150–0.276)[d]	0.378[a]	0.174
601–800	0.193 (0.123–0.263)	0.132	0.077[b]	0.006 (0–0.017)[c] 0.006 (0–0.018)[d]	0.234[a]	0.180[a]
801–1000	0.122 (0.064–0.180)	0.156	0.079	0[d]	NA	0.181[a]
1001–1200	0	0.133[a]	0.105[a]	0[d]	NA	0.186[a]
1201–1400	0	0.093[a]	0.081[a]	0[d]	NA	0.111[a]
>1400	0	0.034[a]	0.048[a]	0[d]	NA	0.022[a]

[a] Observed usage is significantly lower than expected ($P<0.05$).

[b] Observed usage is significantly higher than expected ($P<0.05$).

[c] Study area = composite home range. Only four elevation classes were available in the northwest study area when the composite home range was used.

[d] Study area = delineated habitat (eight elevation classes available, as for the southeast study area).

chance, depending on the method of study area delineation (Table 2). Regardless of method, however, they used low elevations (0–200 m) and high elevations (>1000 m) less than would be expected by chance. The use of high elevation (>1000 m) habitat by NW females was also low relative to availability, but they differed from SE females in using the lowest elevation class (0–200 m) more than would be expected by chance.

When elevation was analyzed by season, females in the SE subpopulation consistently used higher elevation habitat than females in the NW subpopulation (Fig. 2c). When habitat use was evaluated using the composite home range of the subpopulation, SE females used the two elevation categories (0–400 and ⩾401 m) in proportion to availability during all seasons. When habitat selection was repeated using our approximation of available habitat, SE females used the lower elevation category (0–400 m) less than expected by chance during May–July. However, NW females selected this lower elevation category, and used elevations ⩾401 m less than expected by chance, during all four seasons, regardless of how the study area was delineated. Females in the NW subpopulation used lower elevations during fall and winter, than in spring or summer (Fig. 2c).

The availability of elevation classes differed significantly between the NW and SE study areas (Chi-

Table 3
Seasonal selection of slope and elevation by bighorn sheep females in two subpopulations in the Santa Rosa Mountains, Peninsular Ranges, California (1994–1997)

	Southeast subpopulation			Northwest subpopulation		
	Observed proportion of usage (95% C.I.)	Expected proportion of usage, study area = composite home range	Expected proportion of usage, study area = delineated habitat	Observed proportion of usage (95% C.I.)	Expected proportion of usage, study area = composite home range	Expected proportion of usage, study area = delineated habitat
Slope (%)						
February–April						
0–100	0.140 (0.030–0.250)	0.390[a]	0.450[a]	0.281 (0.153–0.409)	0.552[a]	0.636[a]
101–180	0.368 (0.215–0.521)	0.443	0.376	0.493 (0.351–0.635)	0.352	0.318[b]
>180	0.491 (0.332–0.650)	0.167[b]	0.174[b]	0.225 (0.106–0.344)	0.096[b]	0.046[b]
May–July						
0–100	0.080 (0.005–0.155)	0.390[a]	0.450[a]	0.457 (0.341–0.573)	0.552	0.636[a]
101–180	0.293 (0.167–0.419)	0.443[a]	0.376	0.286 (0.180–0.392)	0.352	0.318
>180	0.627 (0.493–0.761)	0.167[b]	0.174[b]	0.257 (0.155–0.359)	0.096[b]	0.046[b]
August–October						
0–100	0.156 (0.047–0.265)	0.390[a]	0.450[a]	0.461 (0.334–0.588)	0.552	0.636[a]
101–180	0.500 (0.351–0.649)	0.443	0.376	0.371 (0.248–0.494)	0.352	0.318
>180	0.344 (0.202–0.486)	0.167[b]	0.174[b]	0.169 (0.074–0.264)	0.096	0.046[b]
November–January						
0–100	0.048 (0–0.127)	0.390[a]	0.450[a]	0.429 (0.260–0.598)	0.552	0.636[a]
101–180	0.619 (0.440–0.798)	0.443	0.376[b]	0.367 (0.202–0.532)	0.352	0.318
>180	0.333 (0.159–0.507)	0.167	0.174	0.204 (0.066–0.342)	0.096	0.046[b]
Elevation (m)						
February–April						
0–400	0.386 (0.242–0.530)	0.287	0.465	0.577 (0.446–0.708)	0.388[b]	0.146[b]
⩾401	0.614 (0.470–0.758)	0.713	0.535	0.423 (0.292–0.554)	0.612[a]	0.854[a]
May–July						
0–400	0.240 (0.130–0.350)	0.287	0.465[a]	0.781 (0.691–0.871)	0.388[b]	0.146[b]
⩾401	0.760 (0.650–0.870)	0.713	0.535	0.219 (0.129–0.309)	0.612[a]	0.854[a]
August–October						
0–400	0.400 (0.264–0.536)	0.287	0.465	0.888 (0.813–0.963)	0.388[b]	0.146[b]
⩾401	0.600 (0.464–0.736)	0.713	0.535	0.112 (0.037–0.187)	0.612[a]	0.854[a]
November–January						
0–400	0.309 (0.150–0.468)	0.287	0.465	0.878 (0.773–0.983)	0.388[b]	0.146[b]
⩾401	0.691 (0.532–0.850)	0.713	0.535	0.017 (0.017–0.227)	0.612[a]	0.854[a]

[a] Observed usage is significantly lower than expected ($P < 0.05$).

[b] Observed usage is significantly higher than expected ($P < 0.05$).

square = 57045.4, d.f. = 4, $P < 0.001$ and Chi-square = 1394.4, d.f. = 7, $P < 0.001$ when availability was evaluated in study areas delineated by the composite home range and our approximation of habitat, respectively; Table 2). Urban areas were typically found at low elevations. Random locations in urban areas had mean elevations of 126.9 m (S.D. = 34.1, range = 77.5–224.8) and 113.2 m (S.D. = 12.3, range = 91.2–137.5) when the study area was delineated as the composite home range of the subpopulation and our approximation of available habitat, respectively.

During our study, 35% (109 of 314) of locations in the NW subpopulation were located within urban areas, indicating a strong selection (Chi-square = 475.17, d.f. = 1, $P < 0.001$) for urban habitat which had a relative availability of only 5.8% when we used the composite home range of the subpopulation to delineate the study area. Availability was even less (1.4%) when we used our approximation of available habitat to delineate the study area. Mean distance from the center of individual core activity areas to the edge of the urban area was 300 m (S.D. = 337 m, $n = 10$ females). For three of the 10 females, the center of their core activity area was located within urban areas. The proportion of NW locations occurring within urban areas was lower in February–April than during other seasons (Fig. 3). Conversely, the mean distance to urban areas was largest during February–April.

Overall, percent fecal nitrogen (%FN) was higher (Mann–Whitney test, $P < 0.001$) in the NW subpopulation (median = 2.24, range = 0.96–3.38, $n = 120$) than in the SE subpopulation (median = 1.76, range = 1.00–3.04, $n = 108$). Although monthly mean values of %FN in the two subpopulations were correlated ($r_s = 0.837$, $P = 0.001$, $n = 12$), %FN values in the NW subpopulation were significantly higher (Mann–Whitney test, $P \leqslant 0.031$) than values in the SE subpopulation during every month except March, April, May, and July (Fig. 4). In the SE subpopulation, %FN values were above their annual mean from February through August (Fig. 4).

Non-native plants were rarely found in fecal samples of SE females, and only represented a small proportion (mean $\leqslant 0.625\%$) of the diet for any one of the 4 months examined. During each of these 4 months, the NW samples contained a minimum of 21% non-native plants. We found the highest proportion of non-native plants in the diet of NW females during March (mean = 40.75%) and June (mean = 46.43%), and these proportions were significantly higher ($P \leqslant 0.044$) than the proportion found in the September samples (mean = 22.22%; Fig. 4). The monthly proportion of NW locations occurring within urban areas was not correlated with monthly mean %FN values for SE females ($r_s = -0.452$, $P = 0.140$, $n = 12$). We also did not find a significant correlation between this proportion and the mean monthly %FN values for females in the NW subpopulation ($r_s = -0.420$, $P = 0.174$, $n = 12$). However, the proportion of locations within urban areas was significantly correlated with the difference between NW and SE mean monthly %FN values ($r_s = 0.599$, $P = 0.040$, $n = 12$).

In the SE subpopulation, the mean monthly minimum distance to water (natural or manmade) was negatively

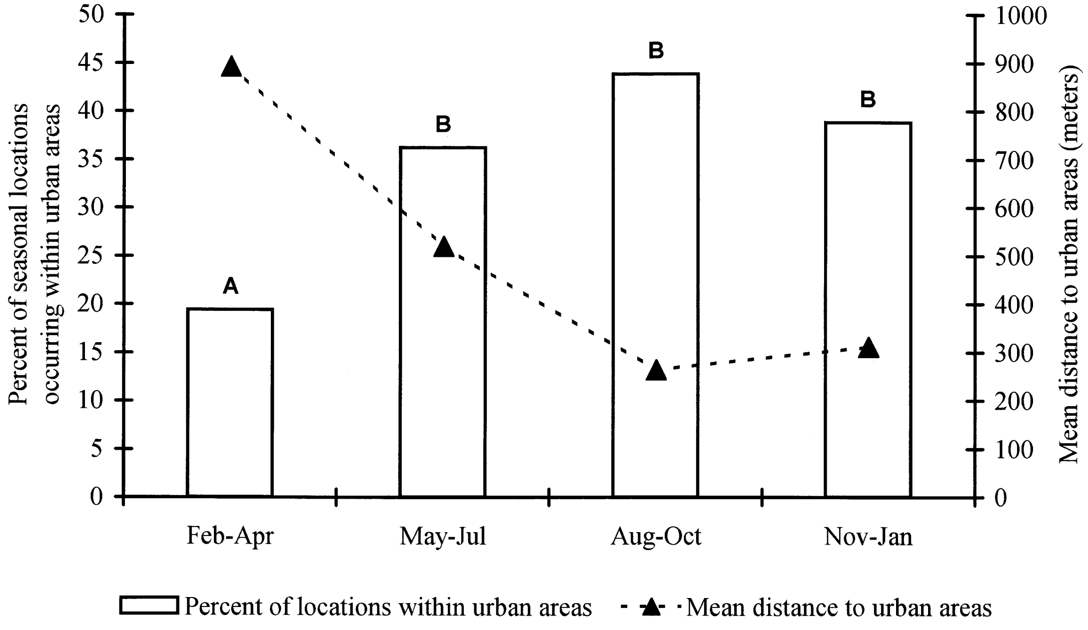

Fig. 3. Percent of female bighorn sheep locations occurring within urban areas, and mean distance (meters) to urban areas, per season, in the northwest (NW) subpopulation in the Santa Rosa Mountains, Peninsular Ranges, California (1994–1997). Seasons sharing the same upper case letter (A, B) were not significantly different from each other (Chi-square test, $P < 0.05$).

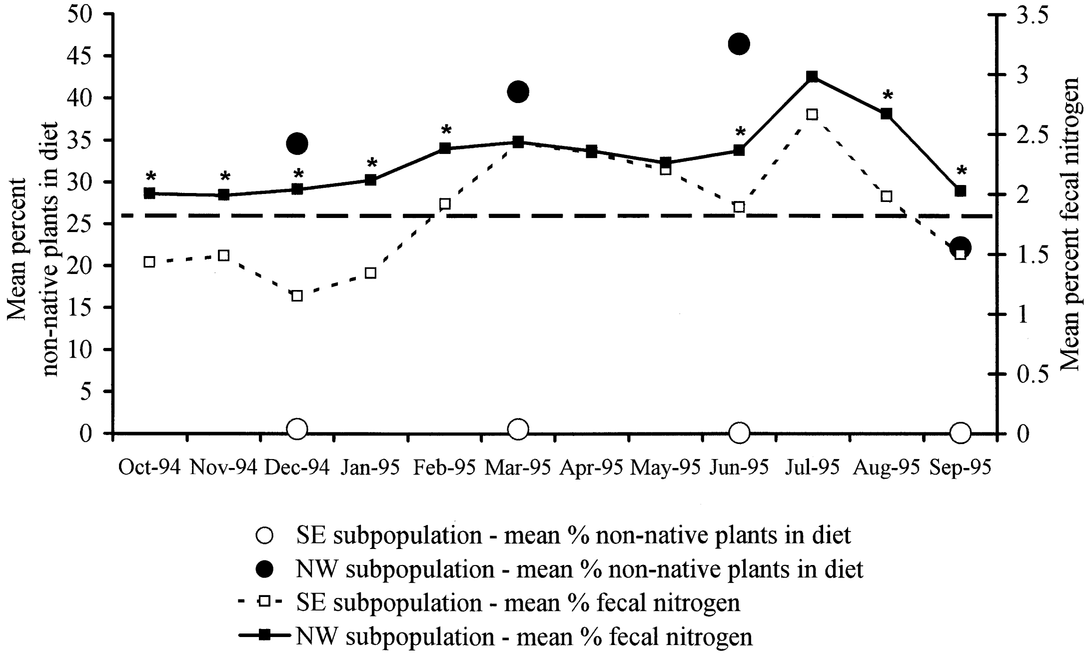

Fig. 4. Mean% fecal nitrogen and% of diet comprised of non-native plants, in bighorn sheep females in two subpopulations in the Santa Rosa Mountains, Peninsular Ranges, California (October 1994–September 1995). Horizontal dashed line indicates annual mean% fecal nitrogen in the southeast (SE) subpopulation. (*) indicates a significant difference between% fecal nitrogen values in the SE and the northwest (NW) subpopulations (Mann–Whitney test, $P<0.05$).

correlated ($r_s=-0.469$, $P=0.049$, $n=18$) with mean monthly high temperature. This correlation became stronger ($r_s=-0.543$, $P=0.020$, $n=18$) when only natural water sources were considered, and no correlation was found when we considered only man-made water sources. We found no correlation between monthly total precipitation and the mean minimum distance of SE females to water (natural and man-made combined), or to natural water. In the NW subpopulation, we found no significant relationships between monthly climate variables and the mean minimum distance to water sources, or to urban areas. The monthly mean minimum distances of SE and NW females to water sources were also not correlated. Females in the SE subpopulation tended to be closest to natural water during May–July and August–October, while females in the NW subpopulation tended to be closest to natural water during February–April (Fig. 2d). On a monthly basis, there was no correlation between the proportion of NW locations within urban areas and the mean minimum distance to natural water among females in the SE subpopulation ($r_s=-0.264$, $P=0.291$, $n=18$).

During our study we examined 77 individual fecal samples for parasites. Parasite examination revealed trichostrongyle type eggs in the NW subpopulation samples during each of the three sampling sessions. In summer 1996, summer 1997, and winter 1997, females in the NW subpopulation had a prevalence of 73% ($n=11$), 25% ($n=8$), and 38% ($n=8$), respectively. Among positive samples, the median number of eggs per gram during each of these periods was 14.5 (range = 2–153), 37.7 (range = 34–42), and 50.0 (range = 17–67), respectively. No trichostrongyle eggs were detected in samples from the SE subpopulation or the Coyote Canyon, Vallecito Mountains, and San Ysidro Mountains subpopulations.

4. Discussion

Because urban development is progressing rapidly throughout much of the world, it is becoming increasingly important to understand how the use of urban environments impacts wildlife populations. While many species avoid urban areas, others continue to use developed areas. Urban developments may attract some species by providing an abundance of food or other resources (Adams, 1994). This attraction can result in habituation and increased fitness in individuals (Thompson and Henderson, 1998) and increased population densities (Riley et al., 1998). For many species and populations, however, the long-term impacts of such an attraction are not well understood. Our study demonstrated that the use of urban areas was associated with altered behaviors in bighorn sheep, which could potentially have long-term impacts on this endangered population.

Although bighorn sheep frequently avoid areas of human activity (Bates and Workman, 1983; Etchberger et al., 1989), bighorn sheep in the NW Santa Rosa Mountains subpopulation were in urban areas during

35% of our observations. Furthermore, bighorn sheep in that subpopulation preferentially selected urban areas relative to their availability. This subpopulation exhibited diet and habitat use patterns distinct from those of the neighboring SE subpopulation, which was never observed in urban areas. Group sizes in the NW subpopulation were smaller overall, but exhibited a peak in August–October that coincided with a peak in the proportion of locations occurring in urban areas (Figs. 2a and 3). Although home range sizes (95% utilization distributions) did not differ between the two subpopulations, core activity areas (50% utilization distributions) were smaller in the NW subpopulation (Table 1). The centers of core activity areas of 10 females were located either within or in close proximity (mean = 300 m) to urban areas, suggesting that use of urban areas may be associated with a contraction of core activity areas. We observed animals repeatedly resting and feeding on a small number of urban lawns, and this behavior may have increased group size and contracted core activity areas.

Optimal foraging theory suggests that animals will prefer those areas that allow them to acquire forage resources most efficiently (MacArthur and Pianka, 1966), and it is likely that manicured urban gardens that are watered and fertilized regularly provided bighorn sheep with a constant and superior forage supply when compared with native desert habitats. Percent fecal nitrogen was higher for NW samples during all months except those (March, April, May, July) when SE sample values reached their highest levels (Fig. 4). Furthermore, the monthly difference between NW and SE mean percent fecal nitrogen (%FN) values was positively correlated with the monthly proportion of NW locations in urban areas, suggesting that the use of urban areas resulted in acquisition of superior forage. It is possible that %FN values were elevated in the NW subpopulation due to high tannin levels in non-native plants (Hobbs, 1987). We therefore examined how urban use and consumption of non-native plants among females in the NW subpopulation was related temporally to the forage quality of native plants, as indexed by %FN values among females in the SE subpopulation. Females in the NW subpopulation exhibited a seasonal pattern in their use of urban areas (Fig. 3), but this temporal pattern did not appear to be related to the forage quality of native plants. Thus, we did not find strong evidence that optimal foraging behavior was solely responsible for the observed selection of urban areas. However, we cannot exclude the possibility that the strategy of optimal foraging behavior was in use but that another currency, such as feeding rate, was being maximized (Schoener, 1971), or that additional resource needs influenced habitat selection.

Water is an important and potentially limiting resource for desert bighorn sheep (Jones et al., 1957; Blong and Pollard, 1968; Leslie and Douglas, 1979; but see Krausman and Leopold, 1986). In the SE subpopulation, distance to water decreased as temperatures increased, and females were found closest to natural water during May–October (Fig. 2d). If urban areas were used by NW females primarily as a water source, use should have been highest during that period. Although use of urban areas peaked during August–October, we did not find correlations between climate variables (temperature and rainfall) and distance to urban areas, or to natural sources of water, in the NW subpopulation. Furthermore, we did not find a significant correlation between the use of urban areas by NW females and the monthly mean distance to water among SE females. We therefore did not find evidence that bighorn sheep in the NW subpopulation used urban areas solely as a water source. It is possible, however, that this relationship was confounded by forage availability within the urban areas.

Although urban areas provide water and forage for bighorn sheep, the use of urban areas may have negative consequences. We found that females in the NW subpopulation used areas with gentler slope and lower elevation than females in the SE subpopulation. Although this finding could be due to differences in availability of slope and elevation classes between the two study areas, our analyses, which account for differences in availability, indicated that the two groups selected different slope and elevation classes (Tables 2, 3). The use of gentler slopes may have implications for survival in the NW subpopulation if animals are located farther from escape terrain. Bighorn sheep are thought to evade predators by using steep slopes (Geist, 1971; Bleich, 1999), and most habitat models for this species identify steep terrain as a key habitat characteristic (McCarty and Bailey, 1994). Predation by mountain lions *Puma concolor* was the primary cause of mortality among adult radiocollared bighorn sheep in the Peninsular Ranges during 1992–1998 (Hayes et al., 2000), indicating that predation risk was high during our study. However, survival rates for adults in the two subpopulations (0.76 in the SE subpopulation and approximately 0.81 in the NW subpopulation; Hayes et al., 2000; Ostermann et al., 2001) do not suggest that the use of lower slope increased mortality rates among adult females in the NW subpopulation. Nonetheless, it is possible that lambs were placed at higher risk. During our study, lamb survival was low in the NW subpopulation relative to three other subpopulations studied, including the SE subpopulation (43.5% of lambs survived to 3 months of age between 1993 and 1996, compared with 86.9% in the SE subpopulation; Rubin et al., 2000). Although disease processes may contribute to the observed low recruitment (DeForge et al., 1982), altered habitat selection may also put lambs at increased risk of predation. Indeed, Bleich (1999) reported that mortality rates of bighorn lambs due to coyote predation tended to be higher in open (flat or rolling) terrain than in steep terrain. However, the causes of lamb mortality in the Peninsular Ranges are not well understood and should be investigated because recruitment rates represent a major difference between the NW and SE subpopulations, and they may be influenced by the selection of urban areas.

Patterns of habitat use may increase the risk of disease among bighorn sheep in the NW subpopulation because the smaller core activity areas and repeated use of selected urban areas may facilitate disease transmission (May and Anderson, 1979). Trichostrongyle parasites, which were found only in the NW subpopulation, may provide one example. It is quite likely that parasite transmission was promoted by environmental conditions (frequently watered lawns versus the more typical arid desert bighorn sheep habitat) because warm moist conditions are favorable for the development of trichostrongyle larvae (Levine, 1963). Transmission may also have been increased among bighorn sheep feeding and defecating (and thus shedding parasite eggs) repeatedly on the same lawns. Parasites may reduce an animal's resistance to other pathogens, or directly impact survival or reproduction of a population (Scott, 1988). In addition to predation and disease, bighorn sheep in the NW subpopulation are at risk of urban related injuries and mortalities, such as collisions with cars and consumption of toxic plants (Bighorn Institute, 1999).

We found that females in the NW subpopulation used urban areas least during February–April (Fig. 3). This was the only season during which NW females selected the same slope classes as SE females. This season corresponds to the peak months of birth for bighorn sheep in the Peninsular Ranges (Rubin et al., 2000), and it is possible that the use of urban areas declined as females sought steeper or more secluded terrain prior to giving birth (Geist, 1971). In the NW subpopulation, the increased use of urban areas in the summer coincided roughly with the loss of a number of lambs. It is not clear from our data, however, if the loss of lambs was associated with urban use or if females were simply returning to urban areas after losing their lambs to other causes.

Bighorn sheep have been observed in urban areas in the NW Santa Rosa Mountains since 1965 when an artificial water source was established for their use at the edge of one housing development (Blong, 1967). It is possible that bighorn sheep in this subpopulation used lower slopes than animals in the SE subpopulation did, even prior to the development of this water source. If individual females established home ranges near this water source and became accustomed to using urban areas, the philopatric behavior of bighorn sheep (Geist, 1971) may have maintained these habitat use patterns for many generations. It is likely that the selection of slope and elevation among females in the NW subpopulation is related to their use of urban areas. This subpopulation has been augmented with captive-raised sheep since 1985 (DeForge et al., 1995) and it is likely that released individuals adopted the habitat use patterns of animals already present in the subpopulation.

Although we did not identify a primary resource attracting bighorn sheep to urban areas, it is clear that both water and forage within the urban areas were being used. Conservation efforts are underway to prevent further conversion of bighorn sheep habitat to urban areas (US Fish and Wildlife Service, 2000). In addition, some existing urban areas have been fenced to restrict access by bighorn sheep and more may be fenced in the future (US Fish and Wildlife Service, 2000). As the availability of urban areas is reduced, habitat use and selection by females in this subpopulation should be monitored to determine whether their habitat use patterns become more similar to those of SE females. Moreover, lamb survival and parasite prevalence should be monitored as urban use decreases; improvements in these measures would suggest that these costs were a consequence of urban use. While our study focused on females, future evaluations should also include the diet and behavioral ecology of males, because male bighorn sheep are known to range farther and to use habitat differently than females (Bleich et al., 1997). In addition, future studies are needed to examine bighorn sheep resource needs. Precautions should be taken when using results of habitat selection analyses to identify areas of important habitat or to delineate areas of habitat protection because essential resources may be used for short time periods only and may, therefore, not be identified as a selected habitat component (White and Garrott, 1990; North and Reynolds, 1996). For example, important water sources may be used only briefly (Morrison et al., 1992), while some habitat areas may provide important forage resources only seasonally or during periodic droughts (Leslie and Douglas, 1979).

Acknowledgements

This project was funded by the California Department of Fish and Game, the Zoological Society of San Diego, the California Department of Parks and Recreation, the Minnesota-Wisconsin Chapter of the Foundation for North American Wild Sheep, the Desert Bighorn Council Hansen-Welles Memorial Fund, and the Sierra Club's San Diego North County Group Bob Davey Memorial Scholarship. Valuable assistance and support were provided by J.L. Allen, V.C. Bleich, M. Fisher, M.C. Jorgensen, and A. Muth, and the cooperation of the Bighorn Institute staff was greatly appreciated. The presence of the University of California's

Philip L. Boyd Deep Canyon Research Center in the Santa Rosa Mountains greatly facilitated this research. V.C. Bleich, E.P. Caswell-Chen, I.A. Gardner, S.D. Ostermann, and P. Sorensen provided valuable suggestions on an earlier draft of this paper.

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