

# GROUP SIZE AND HOME RANGE OF THE ARABIAN WOLF (*CANIS LUPUS*) IN SOUTHERN ISRAEL

REUVEN HEFNER AND ELI GEFFEN

*Nature Reserves Authority, P.O. Box 677, Eilat, Israel (RH)*  
*Institute for Nature Conservation Research, Faculty of Life Sciences, Tel Aviv University,*  
*Ramat Aviv 69978, Israel (EG)*

The Arabian wolf (*Canis lupus arabs*) is a desert-adapted canid that occurs throughout arid regions in the Middle East. We examined group size, home range, habitat selection, and dispersal of Arabian wolves in the southern Negev Desert. We investigated the degree of association between wolves and human habitats. Arabian wolves had extensive dispersal distances (50–200 km). Annual survival rate of adults was 81%, but mortality caused by humans was considerable. Size of foraging group and home range were smaller than generally reported for wolves elsewhere. Arabian wolves in the Negev Desert foraged more than expected in the vicinity of human agricultural settlements.

**Key words:** *Canis lupus*, Arabian wolf, survival, home range, foraging group, Israel

The gray wolf (*Canis lupus*) is one of the most persecuted mammal species. In this century, gray wolves have been eradicated from much of North America and large areas of western Europe (Gittleman and Pimm, 1991; Haber, 1996). In other parts of Europe (e.g., Italy, Spain, and Norway), small or remnant populations have persisted (Blanco et al., 1992; Boitani, 1992). In general, wolves are abundant only in regions where human density is low.

In the Middle East, a small, desert-adapted subspecies, the Arabian wolf (*C. l. arabs*) occurs. These wolves occupy arid flats and mountains throughout deserts of the Arabian Peninsula, Syria, Jordan and Israel (Harrison and Bates, 1991). The Arabian wolf is rare throughout most of the Middle East, with the exception of Israel. In the Arabian Peninsula and Jordan, vast areas are used by the nomadic Bedouin for grazing of livestock, and they consider the wolf to be the major predator of their goats and sheep. Systematic shooting and trapping of Arabian wolves has nearly eliminated this carnivore from most areas in the Middle East (Harrison and Bates, 1991; Nader and Büttiker, 1980). Harassing or killing wolves is prohibited in Israel. As a result, the pop-

ulation of wolves in the Negev Desert is relatively dense; 91–159 individuals in ca. 9,600 km<sup>2</sup> (Shalmon, 1986).

Arabian wolves in the Negev Desert feed mostly on trash, carrion and agricultural products. They occasionally hunt hares (*Lepus capensis*), gazelles (*Gazella dorcas*), ibexes (*Capra ibex*), and livestock (Shalmon, 1986; B. Shalmon, in litt.).

The aim of our study was to investigate ranging patterns and dispersal of Arabian wolves in the Negev Desert. Specifically, we studied size of foraging groups, home range, survival, dispersal, and use of human-dominated habitats. We anticipated that wolves in the southern Negev Desert would occupy relatively small ranges and forage in small groups mostly around human settlements.

## MATERIALS AND METHODS

**Study site.**—The study was conducted in ca. 600 km<sup>2</sup> of the southern Negev Desert. The climate in the region was extremely arid. Mean daily summer temperature and relative humidity were 31.5°C and 29%, respectively. Mean annual precipitation was 30 mm (Karta, 1985). The study area has two distinct sections: the Eilat Mountains Nature Reserve and the bottom of the

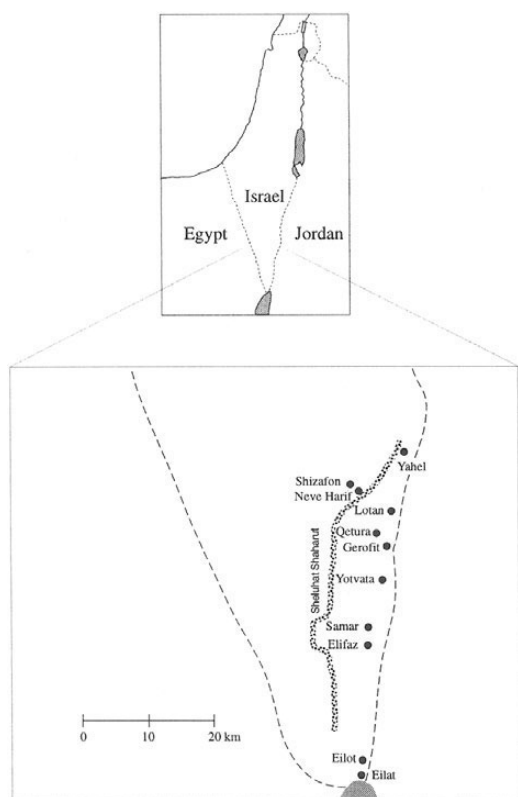


FIG. 1.—Map of the study site in the southern Negev Desert. Dashed lines represent international borders; heavy dotted line indicates the cliff line bounding the Rift Valley to the west. Eilat is a town on the shores of the Gulf of Aqaba; all the others localities are small farming communities.

**Rift depression (Karta, 1985).** The Eilat Mountains Nature Reserve was located along the western side of the Rift Valley, a rugged region of mountains (elevation  $\leq 800$  m) and canyons. The Rift depression north of Eilat (elevation 100 m) was an undulating area of dunes, alluvial fans and flat salt marshes. Most of this area, excluding the relatively sterile salt marshes, was an arid savannah-like habitat. There were eight human settlements in the study site, all situated along the bottom of the Rift Valley. Those communities were agricultural and specialized in dairy products and crops (Fig. 1).

**Field methods.**—Wolves were trapped using Victor #3 SoftCatch leg-hold traps (Woodstream Co., Lititz, PA). Traps were staked to the ground around carcasses of domestic ungulates or ga-

zelles and were observed from a distance at 2-h intervals for several nights. Wolves in our study site were habituated to human presence; hence, our frequent visits did not disturb the animals and enabled us to prevent injury to the trapped wolves. Traps were covered during daylight periods.

Trapped wolves were pinned down by fitting a large plastic bucket over their head and body, and were immobilized with ketamine hydrochloride (10 mg/kg body weight). Wolves were examined for injuries, old scars, and external parasites. We recorded six body measurements and mass, and collected a 10-cc blood sample from each wolf. Age was determined by tooth wear and eruption (Van Ballenberghe and Mech, 1975). Juveniles were considered individuals aged  $<12$  months. Adults were fitted with a 250-g radiocollar (Wildlife Materials Inc., Carbonale, IL). Wolves were kept in a large box trap until they had recovered completely from the anaesthesia and were released at the capture site the same night.

Each radio-collared wolf was monitored for 1–2 nights/month. They were tracked sequentially from a vehicle throughout the night, with locations recorded about every 30 min. Wolves became habituated to our vehicle and were observed with a spotlight from a distance of 50–100 m. We defined a foraging group as a collection of individuals found together during a particular observation; these may not necessarily constitute an entire pack. We recorded size and composition (sex and age) of foraging groups for each observation. In some instances, we could not distinguish sexes, but juveniles  $<8$  months were clearly distinguishable. Because most wolves in our population were unmarked and occasionally we were unable to reliably distinguish between individuals in the dark, the existence of large and stable packs could not be established.

We also used a plane to survey the southern and central Negev Desert in an effort to locate wolves that were known to have dispersed or disappeared from our study site. During the study period, we conducted five aerial surveys at 6–8 month intervals. These surveys were carried out in the early morning when we suspected that wolves would most likely to be foraging in open habitats.

**Data analysis.**—Mean daily activity time was compiled only from night observations when in-

dividual wolves were sequentially tracked. Those activity durations were divided into four seasonal groups and compared using a Kruskal-Wallis test (Sokal and Rohlf, 1995). To examine seasonal changes in the pattern of activity, we summed the total number of active locations per hour of the night, partitioned those into four seasonal groups, and compared among seasons using a chi-square test (Sokal and Rohlf, 1995). Minimal distance travelled each night was calculated by summing distances between sequential locations collected during each night. We compared nightly distances travelled by adult males and females among seasons by using a two-way analysis of variance (Sokal and Rohlf, 1995).

Home-range size was estimated using the percent minimum convex polygon (MCP) method (Kenward, 1987). Percent values were selected based on plots of cumulative percentage of locations versus home-range size. To calculate the MCP ranges, locations were first ranked according to the distance from an arithmetic mean center of activity, and the 5% most peripheral points were eliminated prior to successive recalculations of the home-range size and the mean arithmetic center of the remaining points. This process was repeated at 5% intervals (Ford and Krumme, 1979; Kenward, 1987). To decide which percentage of MCP to use for each wolf, we examined the relationship between home-range size and percentage of locations used. The cut-off value was the point at which the sharp decrease in home-range size began to moderate. Home-range estimates were corrected for small samples using the method of Gaustad and Mysterud (1995), which calculated expected home-range size based on a regression analysis. The equation we used was  $A'_{(n)} = A_{(n)}e^{(6/n)^{0.7}}$  where  $A_{(n)}$  was the observed area (percent minimum convex polygon) and  $n$  was the number of locations used.

Habitat use was determined by a direct count of visits in each 500- by 500-m grid cell in each individual home range. That cell size was selected because an individual wolf could cover a distance of 500 m in <1 min. Moreover, those large grid cells also accommodated for the small samples for some wolves. To accomplish a smoother representation of habitat use, we applied peripheral influence cells. In that procedure, each of the 8 cells surrounding a cell with a fix was assigned a value of 0.125. Peripheral

cells added around edges of the home range were omitted (Doncaster and Macdonald, 1991). We defined two habitat types: human-dominated (e.g., plantations, settlements, and garbage pits) and natural (undisturbed areas). The observed pattern of habitat use for each wolf was compared with the available habitats in its range using a chi-square test (Manly et al., 1994; White and Garrott, 1990). We estimated annual survival rate from radio-telemetry data using the approach described by Trent and Rongstad (1974). The variance and 95% CI for survival rate were calculated following White and Garrott (1990).

## RESULTS

**Capture, dispersal and survival.**—From July 1991 to November 1995, 38 wolves were trapped, weighed, and measured. The sample included 5 adult males, 11 adult females, 10 juvenile males, and 12 juvenile females. Twenty-three wolves were fitted with radiocollars. Subsequent monitoring revealed the turnover rate of the collared population to be high. Wolves usually dispersed or died in 2–4 years. The status of seven wolves could not be determined within 1 year, four after 2 years, and one after 3 years. Most of those were likely the result of transmitter failures. However, we recorded five deaths and seven instances of long-distance dispersal out of our study site (Table 1). Three of the dead individuals were shot after crossing to Jordan. The seven individuals that dispersed moved 50–150 km N of our study site and settled there. Four dispersed after 2 years and three after 3 years (Table 1). Three of the dispersing individuals were males, and four were females. Those individuals were never observed again at the study site but were known to be alive elsewhere. Annual survival rate was  $0.81 \pm 0.15$  (95% CI). This estimate was based on 12 individuals known to be alive and five recorded dead at the end of the study.

**Activity.**—Wolves were active mostly at night. During the day, they stayed under cover, including bushes, boulders, and shallow caves. Activity started in the late afternoon and ceased in early morning. Only

TABLE 1.—Presence (+) of 23 radio-collared wolves monitored between 1991–1996 at the southern Negev Desert. Reasons for absence are indicated: (1) = moved to Pharan wash, 100 km N, (2) = moved to Ramon crater, 150 km N, (3) = moved to Hayun Wash, 50 km N, (4) = died, and (?) = unknown fate.

Ear tag	Sex	Year					
		1991	1992	1993	1994	1995	1996
449	Female	+ (?)					
354	Female	+	+ (?)				
357	Female	+					
355	Female		+ (?)				
356	Female		+	+ (?)			
425	Male		+	+ (1)			
2	Female		+	+	+ (1)		
15	Female			+	+ (4)		
13	Male			+	+ (1)		
17	Female			+	+ (4)		
11	Male			+	+	+ (2)	
7	Female			+	+	+ (?)	
18	Male			+ (4)			
24	Male				+ (?)		
43	Female				+	+ (?)	
44	Male				+	+ (?)	
42	Female				+	+ (4)	
45	Female				+	+ (4)	
36	Female				+	+	+ (3)
41	Female				+	+ (3)	
33	Female					+ (?)	
40	Female					+	+ (3)
38	Female					+ (?)	

4.3% of 671 locations recorded for 14 individuals during the night were inactive. Further, only three active locations were collected after 0900 h, and only one active location was obtained before 1700 h. Seasonal changes in nightly activity pattern were not detected ( $\chi^2 = 51.6$ ,  $d.f. = 51$ ,  $P = 0.45$ ). Moreover, the proportion of active locations per night was not different among seasons (Kruskal-Wallis test,  $H = 2.0$ ,  $d.f. = 3$ ,  $P = 0.57$ ). Mean distance travelled each night was  $13.7 \pm 6.7$  km ( $n = 38$  complete nights), with 41.8 km the longest distance recorded in a single night. Seasonal differences in distance travelled were not detected ( $F = 0.4$ ,  $d.f. = 3$ ,  $P = 0.77$ ). Males and females travelled similar distances ( $F = 0.6$ ,  $d.f. = 1$ ,  $P = 0.44$ ).

**Group size.**—Wolves travelled in small groups (Fig. 2). Mean foraging group size was  $3.2 \pm 2.4$  ( $n = 139$ ). On average,

groups contained  $1.3 \pm 0.7$  adult males and  $1.3 \pm 0.5$  adult females. Additionally, 74.6% ( $n = 67$  observations) and 83% ( $n = 65$ ) of foraging groups (where we were able to identify individual sex) had a single adult male and a single adult female, respectively. About 23% of our observations were of a lone wolf, and 69% were groups of 1–3 wolves. The only two known packs, where all individuals were radiocollared, consisted of three individuals each (two males and a female in one; two females and a male in the other). Overall, no seasonal change in foraging group size was detected (Kruskal-Wallis test,  $H = 5.4$ ,  $d.f. = 3$ ,  $P = 0.14$ ; Fig. 2). Number of adult females per group was similar at all seasons ( $H = 1.6$ ,  $d.f. = 3$ ,  $P = 0.66$ ; Fig. 2); however, number of adult males per group was larger during winter ( $H = 9.5$ ,  $d.f. = 3$ ,  $P = 0.02$ ; Fig. 2). To examine stability of foraging

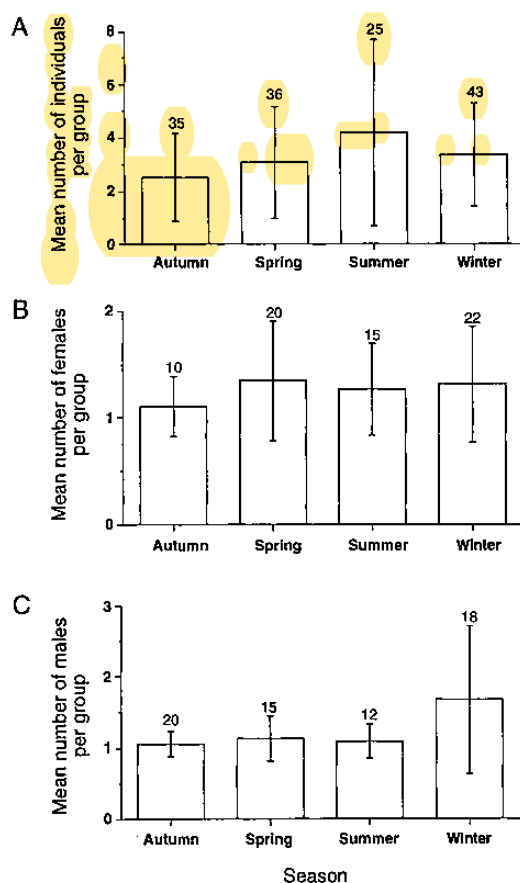


FIG. 2.—A) Mean ( $\pm$  SD) seasonal number of individuals per foraging group, B) Mean seasonal number of females per group, and C) Mean seasonal number of males per group. Number of observations per season is indicated above bars.

groups, we investigated change in group size as a function of time passed since the onset of activity. Total number of individuals per group (Spearman rank correlation,  $r_s = -0.18$ ,  $P = 0.04$ ) decreased with time, but the numbers of males ( $r_s = -0.14$ ,  $P = 0.28$ ) and females ( $r_s = -0.08$ ,  $P = 0.54$ ) were not correlated with the amount of time that passed since the start of activity.

**Home range and habitat use.**—We calculated MCP home ranges using nearly all locations (90–100%). A moderate slope was detected at the 70% level for only one wolf (Table 2). The mean MCP home-range size for seven wolves with adequate number of locations for this analysis was  $22.0 \pm 11.3$  km<sup>2</sup> (Table 2). The expected polygon estimates, a correction for small sample size, averaged  $34.6 \pm 19.5$  km<sup>2</sup> (Table 2).

Analysis of range utilization indicated that active wolves spent on average  $52.3\% \pm 20.7$  of their foraging time in the vicinity of human settlements (Fig. 3). Two settlements (Gerofit and Qetura) were small farming communities surrounded by fields and had livestock housed in small enclosures. Another site that was frequently visited was Sheluhat Shaharut, a 400–700-m high cliff extending along the west side of the Rift depression (Fig. 1). Wolves spent most of the daytime hours (while inactive) at the base of the cliff (Fig. 3). The other four wolves we tracked (Gb, Gl, Yr, and Yt) also exhibited peak activity near human set-

TABLE 2.—Home-range size of seven wolves radiotracked in the southern Negev Desert. Home range was estimated using percent minimum convex polygon (MCP). Expected polygons were calculated following Gautestad and Myrsetrud (1995).

Wolf	Date	Locations		Observed MCP size		Expected MCP size (Km <sup>2</sup> )
		Used	Total	%	Km <sup>2</sup>	
Ml	December 1991–March 1992	49	52	95	5.3	7.9
Hi	March 1992–December 1992	133	140	95	21.5	26.1
Gr	February 1992–October 1993	166	175	95	27.3	32.3
Yt	October 1994–December 1994	22	25	90	32.9	65.5
Yr	July 1994–October 1994	30	43	70	17.5	30.5
Gb	May 1994–June 1994	22	25	90	12.5	24.9
Bl	June 1993–December 1994	48	48	100	37.1	55.3



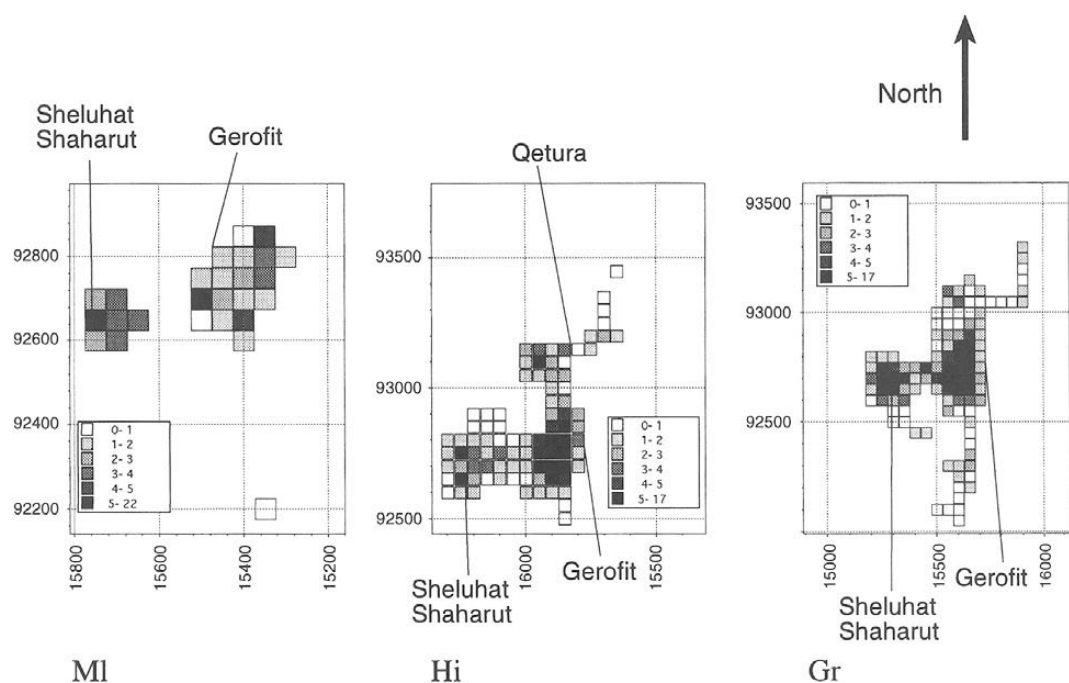


FIG. 3.—Habitat use based on 500 by 500 m grid cells for three Arabian wolves (MI, Hi, and Gr) at the southern Negev Desert. Tick marks and values indicate longitudinal and latitudinal coordinates on the Israel cartographic grid; for MI, minor ticks represent 400-m intervals and for Hi and Gr, 1,000-m intervals. Frequency of visits per cell is illustrated by shading intensity. Gerofit and Qetura are small farming communities, and Sheluhat Shaharut is a cliff of several hundred meters bounding the Rift Valley to the west.

tlements and fields within the study area. On average,  $24.0\% \pm 10.7$  of the area in a home-range was human-dominated habitat. Comparisons between observed and expected distribution of locations indicated that five wolves selected human-influenced habitats (Gl, Gr, Hi, Yr, Yt;  $\chi^2 \geq 14.4$ ,  $d.f. = 1$ , all  $P < 0.001$ ). Two other wolves that occupied the smallest ranges did not select human settlements (Gb and MI;  $\chi^2 \leq 1.8$ ,  $d.f. = 1$ , all  $P \geq 0.18$ ).

#### DISCUSSION

In most areas where wolves exist, humans were the major mortality factor (50–80%; Boitani, 1992; Fritts and Mech, 1981; Fuller, 1989; Nader and Büttiker, 1980; Peterson, et al., 1983). Of the five mortalities of wolves recorded in our study, three were shot, one died of old age, and the cause of

death for the last was unknown. Mech (1970) suggested an overall survival rate of 80% for adult wolves in Minnesota. Annual survival estimates of 72% ( $n = 35$ —Fritts and Mech, 1981) and 64% ( $n = 81$ —Fuller, 1989) were calculated from a large number of radiocollared adult wolves in Minnesota. The annual survival rate observed for Arabian wolves in our study area was similar to those estimates ( $\chi^2 = 1.8$ ,  $P = 0.41$ ).

A wolf pack is generally composed of related individuals, excluding the mating pair (Mech, 1970, 1974; Smith et al., 1997). Studies on wolf populations in North America indicated that group size may vary between 2–20 and may be related to food availability or the size of prey (Zimen, 1976; Peterson, 1977). Arabian wolves in the southern Negev Desert travelled in small packs (3–4 individuals), and the large-

est group we observed was 17. Aggregation into large groups occurred only when food was abundant (i.e., around a carcass or at a garbage pit). Shalmon (1986) reported that 78.7% ( $n = 145$  observations) of foraging groups he observed at our study site numbered three or less individuals. Group size, on average, did not fluctuate throughout the year. The only change that we detected was an increase in the number of males during winter—a change that may be associated with the mating season.

Most groups had a single pair of adults. Shalmon (1986) observed a single wolf in 27% of observations ( $n = 155$ ), pairs (i.e., adult male and adult female) in 19.3%, and an adult female with a juvenile in 14.2% of cases. Groups of two adult males and an adult female or a single adult male with two adult females were recorded in 11.6% of observations. Considering that most of the wolves in our population were unmarked and that we were unable to reliably distinguish between individuals in the dark, the existence of large and stable packs could not be established beyond doubt. However, in most cases, foraging groups were small and inconsistent in composition, indicating that the need to form large and stable packs is reduced compared with wolf populations observed in North America. We seldom observed foraging groups being rejoined by other group members during daytime. In Italy, where wolves have lived with humans for centuries, foraging groups are small, one or two individuals (Boitani, 1992; Zimen and Boitani, 1979). These individuals rejoin the rest of the pack (which usually consists of two to four animals) upon return from night wanderings. Boitani (1992) believed that strategy allowed wolves to move safely in areas populated by humans. Foraging in small groups can be explained by the fact that the wolves in the Rift Valley are largely omnivorous and feed mostly on surplus human production, contrary to most known wolf populations that actively hunt ungulates, beavers (*Castor canadensis*) or livestock (Carbyn, 1987).

Arabian wolves in the southern Negev Desert occupied considerably smaller home ranges than reported elsewhere (Boitani, 1992; Carbyn, 1987). A single adult female that was monitored for 7 months in the central Negev Desert during 1982 occupied 60.3 km<sup>2</sup> (Afik, 1983). In North America wolves that prey on deer (*Odocoileus* sp.) have territories as small as 125 km<sup>2</sup>, but populations that prey on larger ungulates tend to occupy larger ranges (1,250–1,400 km<sup>2</sup>; Carbyn, 1987). The small home ranges of the Arabian wolf probably reflect the clumped distribution of the main food source, which is often located near the settlements along the Rift Valley. Furthermore, we suspected that territory boundaries at our study site are infrequently defended against neighboring wolves, especially around rubbish pits and fields where food is abundant and its renewal rate is high and stable.

Our results imply that the Arabian wolves in the southern Negev Desert have become habituated to the intensive usage of their habitat by humans. Arabian wolves are largely omnivorous and opportunistic feeders. A detailed analysis of 777 wolf scats in the southern Negev Desert revealed that 51.4% contained vegetative material, 37.2% human garbage, and 62.5% hair from cow carcasses (Shalmon, 1986). Only 6.3% of scats contained native mammals (gazelles, hares), excluding small rodents. Carrion was obtained at pits where dead livestock were frequently dumped. The above findings suggest that most food of wolves was scavenged. Such dietary composition has apparently enabled the Arabian wolf to live around humans but avoid conflict by shifting away from systematic predation on livestock. Reports of wolves in North America feeding on garbage are sparse (Grace, 1976; Mech and Hertel, 1983), but Italian wolves obtain 60–70% of their food from the open garbage dumps of nearby villages (Boitani, 1992).

Mendelsohn (1982) classified the wolf population of the Negev Desert into two

separate populations. Our data on dispersal distances of wolves suggested that this division is probably not justified. We recorded four individuals (17.4% of the collared individuals) that dispersed 100–150 km N of our study site. Population genetics theory predicts that only a few migrants are sufficient to prevent significant divergence among subpopulations resulting from random genetic drift (Hartl, 1988). The number of individuals exchanged per average wolf lifetime (ca. 5 years) between the two wolf populations in the Negev Desert is probably greater than a few individuals. Therefore, it is unlikely that these wolf populations can remain genetically separated with such a high exchange rate. Furthermore, the range of body weights of adult male and female wolves at our study site were not different from the values outlined by Mendelssohn (1982) for the desert *C. l. pallipes* (males, 19.0–27.0 kg,  $n = 5$ , versus 17.4–22.5 kg,  $n = 7$ ; females 15.0–19.0 kg,  $n = 11$ , versus 15.7–18.9 kg,  $n = 6$ ). This evidence suggests that wolves in the Negev Desert should be considered as a single continuous population.

#### ACKNOWLEDGMENTS

We thank R. Ben-Shahar, T. Fuller, T. Meier, B. Shalmon, and Y. Shkedy for critically reading this manuscript. R. Ben-Shahar, G. Evron, and M. Ucko assisted with the field work and data collecting. The Fauna and Flora Preservation Society funded some of our telemetry equipment. The Nature Reserves Authority kindly funded field work and occasional aerial surveys.

#### LITERATURE CITED

- AFIK, D. 1983. Movements of a radio-collared wolf (*Canis lupus pallipes*) in the Negev highlands, Israel. *Israel Journal of Zoology*, 32:138–146.
- BLANCO, J. C., S. REIG, AND L. DELACUESTA. 1992. Distribution, status and conservation problems of the wolf, *Canis lupus*, in Spain. *Biological Conservation*, 60:73–80.
- BOITANI, L. 1992. Wolf research and conservation in Italy. *Biological Conservation*, 61:125–132.
- CARBYN, L. N. 1987. Gray wolf and red wolf. Pp. 359–377, in *Wild furbearer management and conservation in North America* (M. Novak, G. A. Baker, M. E. Obbard, and B. Malloch, eds.). Ministry of Natural Resources, Toronto, Ontario, Canada.
- DONCASTER, C. P., AND D. W. MACDONALD. 1991. Drifting territoriality in the red fox, *Vulpes vulpes*. *The Journal of Animal Ecology*, 60:423–439.
- FORD, R. G., AND D. W. KRUMME. 1979. The analysis of space use patterns. *Journal of Theoretical Biology*, 76:125–155.
- FRITTS, S. H., AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs*, 80:1–79.
- FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, 105:1–41.
- GAUTESTAD, A. O., AND I. MYSTERUD. 1995. The home range ghost. *Oikos*, 74:195–204.
- GITTLEMAN, J. L., AND S. I. PIMM. 1991. Conservation biology—crying wolf in North America. *Nature*, 351:524–525.
- GRACE, E. S. 1976. Interactions between men and wolves in the Arctic outpost in Ellesmere Island. *The Canadian Field Naturalist*, 90:149–156.
- HABER, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. *Conservation Biology*, 10:1068–1081.
- HARRISON, D. L., AND P. J. J. BATES. 1991. The mammals of Arabia. *Harrison Zoological Museum, Kent, United Kingdom*.
- HARTL, D. L. 1988. A primer of population genetics. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- KARTA (FIRM). 1985. Atlas of Israel. Macmillan Publication Company, New York.
- KENWARD, R. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. Academic Press, London, United Kingdom.
- MANLY, B., L. MCDONALD, AND D. THOMAS. 1994. Resource selection by animals. Chapman and Hall, London, United Kingdom.
- MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, New York.
- . 1974. *Canis lupus*. *Mammalian Species*, 37:1–6.
- MECH, L. D., AND H. H. HERTTEL. 1983. An eight-year demography of a Minnesota wolf pack. *Acta Zoologica Fennica*, 174:249–250.
- MENDELSSOHN, H. 1982. Wolves in Israel. Pp. 173–195, in *Wolves of the world: perspectives of behavior, ecology and conservation* (F. H. Harrington and P. C. Paquet, eds.). Noyes Publications, Park Ridge, New Jersey.
- NADER, L. N., AND W. BÜTTIKER. 1980. Records of the Arabian wolf, *Canis lupus arabs*, from Saudi Arabia. Pp. 405–411, in *Fauna of Saudi Arabia* (W. Wittmer and W. Büttiker, eds.). Pro Entomologia, Natural History Museum, Basel, Switzerland.
- PETERSON, R. O. 1977. Wolf ecology and prey relationships on the Isle Royale. United States National Parks Service, Scientific Monograph Series, 11:1–210.
- PETERSON, R. O., T. N. BAILEY, AND J. D. WOOLINGTON. 1983. Wolf management and harvest patterns on the Kenai National Wildlife refuge, Alaska. Pp. 96–99, in *Wolves in Canada and Alaska: their status, biology*



- ogy and management (L. N. Carbyn, ed.). Canadian Wildlife Service, Report Series, 45:1–135.
- SHALMON, B. 1986. Wolves in the southern Arava. *Re'em*, 5:60–74. (In Hebrew).
- SMITH, D., ET AL. 1997. Is inbreeding common in wolf packs? *Behavioral Ecology*, 8:384–391.
- SOKAL R. R., AND F. J. ROHLF. 1995. *Biometry: the principles and practices of statistics in biological research*. W. H. Freeman and Company, New York.
- TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. *The Journal of Wildlife Management*, 38:459–472.
- VAN BALLEMBERGHE, V., AND D. L. MECH. 1975. Weight, growth, and survival of timber wolf pups in Minnesota. *Journal of Mammalogy*, 56:44–63.
- WHITE, G. C., AND R. A. GARROTT. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, California.
- ZIMEN, E. 1976. On the regulation of pack size in wolves. *Zeitschrift für Tierpsychologie*, 40:300–341.
- ZIMEN, E., AND L. BOITANI. 1979. Number and distribution of wolves in Italy. *Zeitschrift für Säugetierkunde*, 40:102–112.

*Submitted 6 September 1997. Accepted 6 May 1998.*

*Associate Editor was John A. Litvaitis.*