

Social and ecological influences on dispersal and philopatry in the plateau pika (*Ochotona curzoniae*)

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Benefits and costs of dispersal and philopatry of the social plateau pika (*Ochotona curzoniae*) were studied on the Tibetan plateau for 3 years. Although short-lived, plateau pikas live in cohesive family groups that occupy burrow systems in sedge meadow habitat. Most (57.8%) plateau pikas were philopatric, and dispersal movements were extremely restricted. No juvenile females or adult pikas moved more than two family ranges between years; the greatest observed dispersal distances were by two juvenile males that moved five family ranges from the family of their birth. Traversing unfamiliar habitat was not a cost of pika dispersal because most dispersers settled in families that they could easily visit before dispersal. Dispersal movements appeared to result in equalization of density among pika families, an expected result if competition for environmental resources influenced dispersal. Males did not disperse to gain advantages in competition for mates, as evidenced by their moving to families with significantly fewer females. Females, however, moved to families with significantly more males. Males provide abundant paternal care, and significantly more offspring per female survived to become adults from families with more adult males per adult female. Evidence concerning the influence of inbreeding avoidance on natal dispersal was indirect. Some males exhibited natal philopatry; thus some families had opportunity for close inbreeding. Males and females that dispersed had no opposite-sex relatives in their new families. Philopatric pikas may have benefited by remaining in families that exhibited low local densities, and philopatric females might have benefited from social cooperation with relatives. *Key words*: black-lipped pika, China, dispersal, inbreeding, mate competition, *Ochotona curzoniae*, philopatry, plateau pika, resource competition, Tibetan plateau. [*Behav Ecol* 9:622–635 (1998)]

Why do animals disperse away from where they were born, possibly risking mortality or lost breeding opportunities in unfamiliar habitat, in search of a new home that they might not even find? This question has been the focus of extensive research on the behavioral ecology of birds and mammals (e.g., reviews by Chepko-Sade and Halpin, 1987; Dobson, 1982; Gaines and McClenaghan, 1980; Greenwood, 1980; Greenwood and Harvey, 1982; Johnson and Gaines, 1990; Moore and Ali, 1984; Stenseth and Lidicker, 1992). Factors in the social and ecological environment that influence natal dispersal provide potential explanations for the evolutionary maintenance of dispersal behavior (Anderson, 1989; Cockburn et al., 1985; Dobson, 1979, 1982; Dobson and Jones, 1985; Shields, 1987; Smith, 1987, 1993). In addition, dispersal movements are invoked as major influences on mating systems (Shields, 1987; Waser and Jones, 1983), the regulation of population size (e.g., Gaines and McClenaghan, 1980; Lidicker, 1975, 1985), gene flow and genetic differentiation of populations (e.g., Chepko-Sade et al., 1987; Chesser, 1991; Slatkin, 1985, 1987; Thornhill, 1993), and regional saturation of habitat (Gadgil, 1971; Hanski and Gilpin, 1997; Smith, 1980; Smith and Gilpin, 1997).

Several benefits might accrue to successful dispersers and

thus favor the evolutionary maintenance of dispersal behavior (e.g., Dobson, 1982; Dobson and Jones, 1985; Dobson et al., 1997; Shields, 1987; Smith, 1993): reduced competition for environmental resources such as food, reduced competition for social resources such as mates, and minimization of inbreeding. If environmental resources such as food, nest sites, or refuges from predators limit the size of populations, then individuals might be expected to compete for such critical resources (e.g., Boutin, 1990; Dobson, 1995). Juveniles or subadults might be expected to be poor competitors for these critical resources (Anderson, 1989; Waser, 1985; Wiggett and Boag, 1992; but see Wolff, 1993), and those that leave their natal range might find a new home that has either superior resources or a lower number of conspecifics competing for local resources. Naturally, the same reasoning could be applied to older individuals that move from one home range to another. Thus, advantages gained in competition for environmental resources might explain why some individuals disperse.

In populations that exhibit polygynous or promiscuous mating systems, the number of females attracted as mates may influence male reproductive success and ultimately fitness. Thus, under polygyny and promiscuity, females can be considered "limiting" on the reproduction of males, and males are thus expected to compete for mating opportunities (e.g., Emlen and Oring, 1977; Wittenberger, 1979). Matings might also be difficult for males to obtain under monogamy, if populations exhibit an excess of males. Naturally, under polyandrous mating systems and under monogamy with an excess of females, similar competition for mates might apply to females. Thus, potential mates may be considered important social re-

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sources for which individuals compete. Again, behaviorally subordinate individuals might often be juveniles or subadults, and those that leave their natal home range might find new homes that present better opportunities to acquire current or future mates (Dobson, 1982; Dobson and Jones, 1985; Moore and Ali, 1984). Advantages in competition for mates, therefore, might also explain why individuals disperse.

Dispersal may cause spatial separation of kin that might otherwise mate (e.g., Dobson, 1979, 1982; Dobson and Jones, 1985; Dobson et al., 1997; Pusey, 1987). Offspring of close relatives may suffer lowered fitness due to inbreeding depression (e.g., Harvey and Ralls, 1986; Pusey and Wolf, 1996; Ralls et al., 1986). Inbreeding depression may be caused by the homozygous expression of deleterious recessive alleles in offspring or by heterozygote advantage (e.g., reviews by Mitton, 1993; Waller, 1993). The best examples of inbreeding depression come from breeding programs in zoos (e.g., reviews by Lacy et al., 1993; Ralls et al., 1988), and the influence of inbreeding depression on dispersal patterns in natural populations is controversial (Alberts and Altmann, 1995; Hoogland, 1995; Keane et al., 1996; Packer and Pusey, 1993; Ralls et al., 1986; Rowley et al., 1993; Shields, 1987, 1993; Smith, 1993). If dispersal served to minimize the rate of inbreeding in local populations, then individuals would be expected to disperse before breeding (e.g., Chesser and Ryman, 1986; Waser et al., 1986), and dispersers of any age should find fewer close kin among their potential breeding partners (e.g., Dobson et al., 1997; Hoogland 1995).

In addition to the benefits experienced by successful dispersers, benefits or reduced costs might accrue to individuals that do not disperse but remain philopatric. Such benefits or reduced costs include avoiding mortality risks that dispersal may entail, familiarity with local habitat, and cooperation among relatives, which may increase the probability of survival (e.g., Sherman, 1977; Shields, 1987; Smith, 1987; Waser and Jones, 1983; Waser et al., 1994). Studies of philopatry are relatively uncommon, perhaps due to a bias in interest or because dispersal is easier to identify as an event (Smith, 1993; Waser and Jones, 1983). Particularly for younger animals that have not yet bred, however, the alternatives of dispersal and philopatry should have strong influences on both survival and the likelihood of successful reproduction, and thus on individual fitness (Jones, 1987; Smith, 1987; Waser et al., 1994).

Although there are many exceptions, reviews of dispersal and philopatry in mammalian species reveal a general pattern of predominant dispersal by juvenile or subadult males and predominant philopatry by juvenile females and adults of both sexes (e.g., Chepko-Sade and Halpin, 1987; Dobson, 1982; Greenwood, 1980; Johnson and Gaines, 1990; Moore and Ali, 1984; Stenseth and Lidicker, 1992). Juvenile male dispersal can be attributed to competition for mates and inbreeding avoidance in many species, and philopatric juvenile females and adults may often benefit from familiarity with local habitats and resources (Dobson and Jones, 1985; Waser and Jones, 1983). Because most mammalian species exhibit polygynous or promiscuous mating systems, interspecific studies have examined comparisons to either monogamous mammals or bird species (e.g., Dobson, 1982; Greenwood, 1980). Hypotheses to explain the benefits and costs of mammalian dispersal and philopatry have also been tested intraspecifically (reviewed by Smith, 1993). Intraspecific comparative studies permit examination of patterns of dispersal and philopatry under different conditions in the social and ecological environment.

Most previous intraspecific studies have lacked two kinds of comparisons that could provide powerful insights into the evolutionary maintenance of dispersal and philopatry (for notable exceptions, see Alberts and Altmann, 1995; Waser et al.,

1994). First, the social and ecological environments of home ranges that successful dispersers leave and settle in have rarely been compared (but see Murie and Harris, 1984). This contrast could provide tests of the benefits of dispersal movements. Second, the social and ecological environments for philopatric and dispersing individuals have not been compared. This contrast could provide information about environmental conditions that are most important to individuals, whether they move to a new home range or remain in their present one. The purpose of our study was to examine the environmental circumstances, both social and ecological, of dispersal and philopatry by plateau pikas (*Ochotona curzoniae*, also called "black-lipped pikas"). These comparisons allow us to probe several evolutionary hypotheses that may explain the dispersal movements of the pikas.

METHODS

General biology of the plateau pika

Plateau pikas are small (160 g), nonhibernating, diurnal lagomorphs that inhabit alpine meadows on the Qinghai-Xizang (Tibetan) plateau, People's Republic of China (Smith and Wang, 1991; Smith et al., 1986). Typical of all pika species, plateau pikas are sexually monomorphic in size, and even dimorphism in external sexual anatomy is minimal (Smith, 1988; Smith et al., 1986). The primary social unit is the family of adults and their young that inhabit an interconnected series of burrows on the continuous and generally flat meadows. Within a population, these families are composed of a variable number of breeding adult males and females, and individual families may represent monogamous, polygynous, or polyandrous mating systems (Liang, 1981; Smith and Wang, 1991; Smith et al., 1986; Wang and Dai, 1990; Wang and Smith, 1989). Fecundity within these families is high (Smith, 1988; Smith and Wang, 1991; Wang and Dai, 1991). All adult females reproduce, and three to five sequential litters may be born at 3-week intervals during the summer breeding season. Relative to other pika species, litter size at weaning is large (generally three to six young).

Juvenile pikas do not disperse during the summer of their birth; thus, family size builds throughout the summer (Smith and Wang, 1991). By late summer, population density may range from 100 to over 300/ha (Liu et al., 1981; Shen and Chen, 1984; Smith, 1988; Smith and Wang, 1991; Smith et al., 1986). Members of pika families engage in a broad suite of affiliative behaviors, including allogrooming, alarm calling in the presence of predators, fending off intruders from other families, watching the young of family members, and sitting together in bodily contact (Smith and Wang, 1991; Smith et al., 1986). Overwinter mortality is high, and few adults live to 2 years of age (Wang and Dai, 1989; Wang and Smith, 1988). The sex ratio of surviving animals in a local area may be even or may be skewed in favor of either sex (Wang and Smith, 1988), resulting in the potential for a variety of family mating systems within a population. Dispersal occurs within a narrow window of time just before initiation of the mating season and is not accompanied by the high levels of aggression normally expressed between individuals from different family groups during the remainder of the year (Smith and Wang, 1991; Wang and Dai, 1990). After the mixing that results from dispersal, each newly formed family becomes a cohesive social unit; all individuals have equal access to all resources throughout the family territory (Smith and Wang, 1991). Our study population appeared representative in every way of the general characteristics of these studies of *O. curzoniae* from other sites throughout its geographic range.

Study area

We studied plateau pikas in the northeastern (Amdo) region of the Tibetan plateau, about 30 km east of the village of Shenduo (35°30' N, 101°10' E, elevation 3500 m), Guinan County, Qinghai Province, People's Republic of China. The climate of this part of the Tibetan plateau is dry and cool; most rainfall occurs from June to August, and heavy snowpacks during winter are infrequent (Domrös and Peng, 1988; Watts, 1969; Zong et al., 1986). The range of daily temperatures is great (up to about 25°C), and average annual temperature is about 0°C. Frost may occur in any season, and soils may freeze to a depth of more than 2 m in winter.

Vegetation at the study site was typical of alpine steppe meadow (Zhou and Li, 1982). The meadow consisted of a mosaic of three microhabitat types: (1) meadow dominated by sedges (*Carex* spp., *Kobresia* spp.); (2) large continuous depressions in the sedge meadow dominated in summer by a single species of mint [*Elscholtzia* spp.; because they are barren of vegetation during most of the year, these areas are called "black sands" by the local Tibetans (Ekvall, 1968; Shen and Chen, 1984)]; and (3) small depressions (1–5 m across) in the sedge meadow that contained a variety of grasses and forbs. The habitat was grazed occasionally by domestic herbivores (yak, sheep, and horses) of the indigenous pastoral Tibetans, as well as woolly hares (*Lepus oiostolus*) and zokors (*Myospalax baileyi*). Common predators included weasels (*Mustela altaica*), steppe polecats (*M. eversmanni*), red fox (*Vulpes vulpes*), Pallas' cat (*Otocolobus manul*), black kites (*Mihvus migrans*), and upland buzzards (*Buteo hemilasius*).

The study site lay in the flat bottom of an old stream course approximately 100 m wide. Most of the pika population was observed easily from positions on the edge of the stream course approximately 2 m above the study site, or from locations within the study area. A study area of 4.0 ha was divided into a Cartesian coordinate grid system with 5-m intervals, thus defining 25-m² grid cells. Each grid cell was assigned a unique letter and number code, and all captures and behavioral observations were referenced to their spatial location. Behavioral observations and habitat measurements were focused on a 2.0 ha "core" in the center of the study area.

Sampling procedures

Dates of investigation were 2 April–31 August 1990, 23 May–20 June 1991, and 25 May–9 June 1992. During the 3 years of study, we had 23 field assistants. Work schedules were coordinated so that usually at least four investigators were present on the study area at all times.

We caught pikas in traps or in string nooses that were anchored to the sedge meadow with chopsticks. Several live traps and/or nooses were usually placed around or in burrow entrances in a family area and then observed from about 30 m away. When a pika was captured, it was immediately retrieved and anesthetized with Metofane. Pikas were weighed, examined to determine sex and reproductive condition, and marked for permanent recognition with numbered metal ear tags. Colored plastic disks were affixed to the ear tags to facilitate recognition of individuals during subsequent behavioral observations. Occasionally, the pelage was marked with black fur dye to yield additional unique marks for individual recognition. All animals revived from anesthesia within 10 min of handling and were released at their capture location. We made no focal-animal observations (see below) while animals were being captured on the study site.

In 1990, we marked all animals on the study area. Adults were given a unique combination of ear tag colors. Because of the large numbers of juveniles, we were unable to give each

juvenile a unique color combination. Instead, all juveniles from single litters, which generally emerged from the same burrow and were associated together, were given the same ear tag color combination. Sequential litters born to the same female were given different markings. This procedure allowed us to follow the movements and settlement patterns of juveniles by litter. All juveniles marked in 1990 and surviving to 1991 were captured for identification from their unique ear tag numbers and at that time remarked with unique ear tag color combinations. No juveniles marked in 1990 were captured in 1992 except those also captured in 1991.

We had insufficient time on the study area to mark juveniles in 1991 and 1992. Instead, in 1991 we captured and identified all adult animals on the study area. Some animals had lost both of their ear tags; these were remarked. Some animals had moved onto the greater study area during winter, and these were given new unique ear tag color combinations. In 1992, only previously tagged animals were recaptured to determine their identity unambiguously.

In addition to locating animals on the study area in 1991 and 1992, we conducted regular searches for pikas marked the previous year throughout all habitat within 0.5 km of the study site. Less frequently, observations were made within a radius of several kilometers. When marked animals were located off of the study area, we trapped the other adults in this new family to determine its composition. We then extended our grid to incorporate these new outlying localities and conducted parallel behavioral and spatial observations on the family members there.

Multiple matings within families and extra-familial matings limited our ability to estimate genetic relatedness among individuals (see also Smith and Wang, 1991). Thus, we inferred sibling or half-sibling relationships for offspring of the same mother in 1990. Mothers were identified from field observations of the timing of reproduction and maternal-offspring behaviors and spatial proximity. We classified individuals as putative close relatives if they exhibited a potential coefficient of genealogical relatedness of at least one-quarter (viz., $r = .25$ or $.50$).

Use of space

We determined the use of space by individuals from observed locations of focal animals and scan sampling of all observable animals (Altmann, 1974; Lehner, 1979; Smith and Wang, 1991; Smith et al., 1986). Each 15-min focal observation session was conducted by a quiet and motionless observer from a single location on or adjacent to the study area and commenced after all pikas had grown accustomed to the observer's presence. Several focal individuals were often observed from each location, with haphazard selection of the order in which individuals were observed. The location and behavior of focal animals were observed at 5-min intervals during the 15-min focal-animal sampling periods. We observed each animal repeatedly on different days and at different times of day throughout the study to ensure representation of each age and sex class in the population. A scan sample was conducted after each focal sample. Total focal-animal observation time was 413 h in 1990, 269 h in 1991, and 67 h in 1992. Average number of spatial observations of marked adults (with a period of at least 5 min between observations) was 176.4 ± 10.7 (SE) in 1990, 122.5 ± 4.1 (SE) in 1991, and 42.6 ± 6.2 (SE) in 1992.

We checked interobserver reliability repeatedly throughout the investigation. Both pika identities and grid locations were virtually identical between pairs of observers. Pikas habituated rapidly to observers, and we had no evidence that our presence influenced any aspects of their behavior.

The geometric center of each adult's field of activity was determined using the modified bivariate normal home range program of Koepl et al. (1975), with truncation of the outlying 25% of observations. The relative spacing of all adults on the study area was determined by mapping and measuring the nearest-neighbor distance between centers of activity for various pikas. Spatial overlap among individuals and family groups was determined using the asymmetrical weighted overlap technique of Smith and Dobson (1994). This value incorporates the frequency of use of shared quadrats and reliably reflects the probability of encounters between individuals and groups of animals.

Analysis of behaviors

All occurrences sampling of social behaviors of focal animals within the 15-min observation sessions allowed a detailed portrayal of the interactions among individuals (Altmann, 1974; Lehner, 1979; Smith and Wang, 1991; Smith et al., 1986). Behavioral categories and definitions of behavior followed Smith and Wang (1991). For analyses, we classified the rich behavioral repertoire of the plateau pika as being either affiliative or aggressive behavior (Smith and Wang 1991). To determine the sexual relationships among adults, observed attempted copulations were recorded.

Determination of family composition and location

Family groups were spatially designated as containing pikas whose centers of activity were proximally clustered and which overlapped significantly (Smith and Dobson, 1994). Specifically, average distance between centers of activity of individuals within families was 5.7 m (± 0.25 SE), whereas distances to the nearest individual of each gender outside the family was approximately 25 m (Dobson et al., unpublished data). The geometric centroid for each family home range was determined from the pooled observations of adult pikas in each family. Because juveniles were not individually observed, and juveniles typically use the family range of the adults (Dobson et al., unpublished data; Smith and Wang, 1991;), we assigned the 1990 center of activity for each juvenile as the center of their family range. The average distance separating the centers of activity of neighboring families was 23.8 m (± 0.7 SE, $n = 57$). Locations of families on the study area were spatially consistent among years; an average of only 5.1 m (± 0.8 SE, $n = 26$) separated the geometric centers of families from 1990 to 1991.

Our family designations were corroborated with a posteriori analyses of behavioral interactions within and among families. Within family territories, adults expressed frequent affiliative behavior (99% of all recorded behaviors among adults within families was affiliative rather than aggressive; $n = 1841$). In contrast, the majority of social interactions between adults from different territories was aggressive; for example, 96% of all male aggressive behavior involved males from different families ($N = 345$). We constructed detailed matrices for each year by gender and family for all affiliative and aggressive interactions. All families fit the general pattern of high rates of intrafamily affiliative behaviors and interfamily aggression. In no cases did these behavioral analyses contradict our designation of families using spatial criteria (Dobson et al., unpublished data).

Philopatry and dispersal

Philopatry and dispersal were measured with respect to the observed spacing of family ranges. We observed 39 family groups, including all families into which dispersing pikas set-

led. The clarity with which family ranges could be determined spatially and behaviorally allowed us to determine accurately the actual geometry of spacing of family ranges and their associated burrow systems on the study area. Our primary measure of dispersal was the number of specific family ranges traversed between years. We also present the linear distance between centers of activity of an individual in one year compared to the following year as a secondary measure of dispersal. Philopatry was defined as the presence of an animal in the same family range and burrow system in consecutive years.

Dispersal distances as determined by direct measurement of a fully-marked population may be underestimated compared to actual dispersal distances because of the inability to detect long-distance dispersers (Koenig et al., 1996). Biases imposed by a finite study area may be overcome in two ways: by comparing the number of new individuals entering the study population with those leaving, and by surveying large areas relative to dispersal distances and calculating a correction for bias (such as an area-ratio method; Koenig et al., 1996). We addressed the possibility of long-distance dispersers in three ways. First, we constructed as a part of our active study a buffer zone equal in size and surrounding our core study area that was fully gridded and under observation at all times during scan samples. This secondary study area allowed us to directly monitor movements of animals off of the core study area and to determine the origin of some short-distance dispersers onto the core study area.

Second, a comparison of previously unmarked to marked pikas in 1991 demonstrated a very low rate of immigration into the study population, thus indicating low rates of long-distance dispersal. The study area was part of a large continuous meadow, with no apparent physical barriers to deter dispersal, and the few immigrants to the core study area may well have left nearby families (see below). Third, we attempted to locate as many long-distance dispersers as possible with comprehensive searches within a radius of 0.5 km from the study area, as well as sporadic searches within a distance of several kilometers. Pika habitat and families extended in all directions from the study area and were extremely easy to observe, but emigration was rare (see below).

Habitat variables

Within the mosaic of microhabitats, each family of pikas occupied a landscape that was different from the habitat of other pika families. In addition, many grid cells contained all three of the microhabitat types, although only about half of the grid cells (47.4% of 800 cells) contained black sands microhabitat. We examined the complexion of family home ranges in terms of the amount of each microhabitat type and the extent of habitat composed of edges between different microhabitat types (sedge meadow versus black sands and sedge meadow versus small, mixed-grass and forb depression; black sands and grass/forb depressions did not come into contact). Habitat "edges" may be an important resource because pikas often feed along edges and may be less visible to avian predators when under the overhang of the sedge meadow or in depressions of the other two microhabitats. We tallied two types of burrow entrances: those that connected to the underground burrow system that each family occupied and short "duck holes" that terminated within 0.5 m of the meadow surface and did not connect to the family burrow system. Topography of the terrain of each grid cell was scored as either (1) flat, (2) gently sloping, or (3) sloped.

Adult pikas occasionally were seen outside of their family home range. These observations were particularly common among adult males, who may have been in search of mating

opportunities or were being chased by other males (such chases commonly crossed the entire study area in less than a minute). As these rare locality fixes of adults outside their normal home range could bias comparisons of habitat characteristics among families, we included only those grid cells that contained at least 1.0% of the observations of all adults in the family when characterizing the habitat utilization of each family. This procedure yielded an area of grid cells that were used by most or all of the family members.

Statistical procedures

Statistical procedures were performed using SAS software (SAS Institute, 1989). Statistical significance was accepted at the $\alpha = 0.05$ level, unless several tests were run simultaneously. In the latter case, an adjusted α was defined as $\alpha' = 1 - (1 - \alpha)^{1/k}$, where k was the number of tests run (Sokal and Rohlf, 1981). Parametric procedures were applied to normally distributed data; otherwise nonparametric procedures were applied.

RESULTS

Pika population

Composition of 26 plateau pika families that occurred within our 2.0-ha core area in 1990 varied from a single adult female to a family of two males and three females, and included an increasing number of juveniles as the three spring and summer breeding efforts of the females progressed. As in other studies of the species (Smith and Wang, 1991), juveniles remained within their natal family range during the annual breeding season. Density increased dramatically as the summer of 1990 progressed, from about 40 adults/ha to more than 175 adults and juveniles/ha. Composition of pika families averaged 2.9 adults (1.2 males and 1.7 females) and 10.5 juveniles that survived long enough to be caught.

Overwinter survivorship was low for both juvenile and adult plateau pikas. We did not capture and mark all of the pikas that lived in the 2.0-ha "buffer zone" that surrounded the 2.0-ha core study area. Of the 272 juveniles that we marked in the total 4.0-ha study area during 1990, however, 19% ($n = 51$) survived and could be identified in 1991. Of the 102 adult pikas marked in the 4.0-ha study area in 1990, 17% ($n = 17$) survived and could be identified individually in 1991. Twenty individuals marked in 1990 that survived to 1991 lost both of their ear tags, and we were unable to determine if these pikas had been juveniles or adults in 1990 or to assess their dispersal movements. Thus, combined survival of juvenile and adult pikas from 1990 to 1991 was 23.5% (88/374). From the ear-tagged population of 77 adult pikas in 1991, 22 (28.6%) survived and were captured in 1992.

Philopatry and dispersal

Dispersal distances of pikas were short, and a high proportion of individuals (57.8% of 90 pikas) surviving from one year to the next exhibited familial philopatry (Figure 1). Fewer juvenile males (17.4%) than females (67.9%) exhibited natal philopatry (Figure 1; χ^2 with Yates' correction = 12.9, $n = 23, 28, p < .001$). Among adults, the percentage of breeding philopatry by males (58.3%) and by females (81.5%) was not significantly different ($\chi^2 = 2.3, n = 12, 27, p = .17$).

The remaining 42.2% of plateau pikas dispersed. For juveniles born in 1990 that survived to 1991, dispersing males moved farther than dispersing females (means = 2.00 and 1.11 family ranges, respectively; Figure 2; Wilcoxon test with normal approximation; $n = 19, 9$, respectively; $z = 1.93; p =$

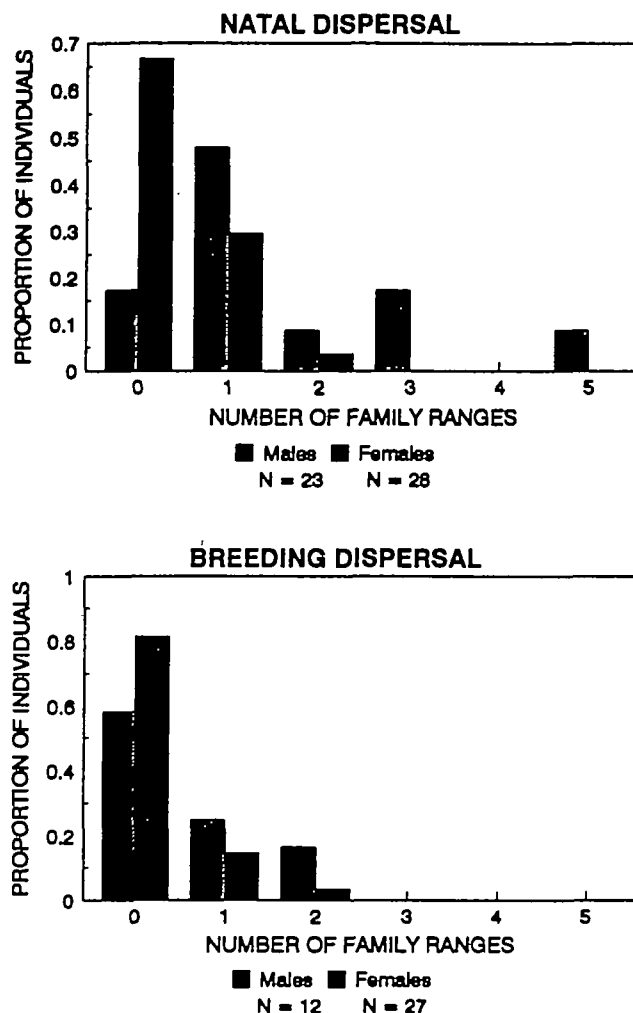


Figure 1
The number of family ranges moved from one year to the next for juvenile pikas (natal dispersal; top, 1990–1991) and adults (breeding dispersal; bottom, 1990–1991 and 1991–1992 combined). Pikas that moved zero family ranges were considered philopatric.

.05). Among adults that dispersed between 1990–1991 and 1991–1992 (pooled samples), distances moved by males and females were not significantly different (male mean = 1.40 family ranges; female mean = 1.20 family ranges; Wilcoxon test; $n = 5, 5$, respectively; $z = 0.52; p = .60$).

The pattern of movements as indicated by the family ranges traversed can also be seen in the composite of both philopatric and dispersing individuals (Figure 2). Composite natal movements by juvenile males (mean = 1.65 family ranges) were significantly greater than those of juvenile females (mean = 0.56 family ranges; Wilcoxon test; $n = 23, 28$, respectively; $z = 3.99; p < 0.0001$). Pooled movements of philopatric and dispersing adults from 1990 to 1992 were not significantly different between males and females (means = 0.58 and 0.22 family ranges, respectively; Wilcoxon test; $n = 12, 27; z = 1.57; p = .12$). Among all males, natal movements were significantly greater than movements of adults (means above; Wilcoxon test; $n = 23, 12$, respectively; $z = 2.88; p = .02$). Among all females, natal movements were not significantly greater than movements of adults (means above; Wilcoxon test; $n = 28, 27$, respectively; $z = 1.08; p = .28$). Movement distances between pika centers of activity in one year and the next exhibited a virtually identical pattern of differ-

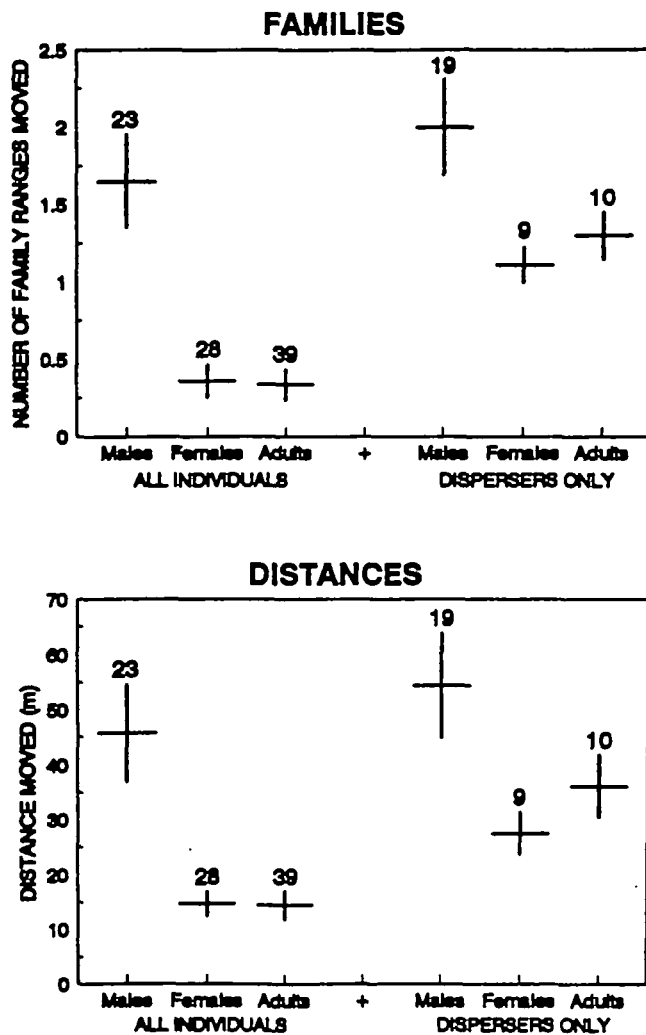


Figure 2
Distances moved (± 1 SE) by pikas from the natal range to their first breeding range for male and female juveniles, and adults (sexes combined). Movement by family ranges is shown at the top, and by linear distance (in meters) at the bottom. Movements of all individuals are shown to the left, and of those individuals that dispersed to a new family on the right. Numbers above the lines indicate sample sizes.

ences between juvenile males, and both juvenile females and adults of both sexes (Figure 2).

Observed natal and breeding dispersal distances (Figures 1 and 2) were not only short in absolute terms, they were extremely restricted relative to the vagility of pikas. Any pika could traverse the breadth of the study area in a few minutes or less (chases between adult males of more than 100 m generally took less than 1 min). Thus, pikas had the opportunity to know the social and physical attributes of other family ranges before dispersing by making short forays from their current family range or even by observation at a distance.

The short dispersal distances of plateau pikas allowed us to closely and accurately monitor dispersal, and indirect evidence also suggested that dispersal was extremely limited. Of 78 adults that lived primarily within the core study area in 1991, only 4 (5.1%) were unmarked immigrants. These immigrant pikas lived at the edges of the core study area, and none of the 15 families in the center of the core area contained unmarked immigrants. Given the density of pika families on the study area, approximately 1400 pika families lived

within the 0.5-km radius extending out from the study area. Only two of these families contained a single juvenile male that had emigrated from the study area (natal dispersal distances of 159 and 160 m). The greatest distance of female natal dispersal, which occurred within the study area, was 56 m. The greatest breeding dispersal movement by a male was 78 m and by a female was 44 m, again movements that took place within the study area. We observed one of the males with the greatest natal dispersal movement to visit his natal family range as an adult, while the other far-dispersing male was not observed to do so. Virtually all dispersing pikas that moved only one or two family ranges between years were eventually seen on some part of their previous natal or breeding family range.

Habitat factors

We examined the relationship between possible habitat resources and the activity of pika families in 1991, when we recorded extensive data on daily activity of pikas over a relatively short period (about 4 weeks). Twenty-six pika families had ranges wholly within the 2-ha core study area where habitat characteristics were recorded. For these families, the number of grid cells in the family range was not associated with the number of observations per individual (Pearson's $r = .077$, $df = 24$, $p = .71$), and thus the size of family ranges was not a function of sampling. Family ranges averaged 28.9 grid cells (0.07 ha), and ranged from 18 to 41 cells. Larger families occupied significantly more grid cells (Figure 3; $R^2 = .41$, $df = 1,24$, $F = 16.67$, $p = .0004$). However, larger families also had fewer grid cells of habitat per individual than smaller families (Figure 3; $R^2 = .72$, $df = 1,24$, $F = 61.89$, $p < .0001$). For the period 1990–1991, family ranges from which juvenile males and females emigrated (viz., ranges in 1990), families to which they immigrated (ranges in 1991), and families of philopatric juveniles (ranges in 1991) did not differ significantly in either area or area per pika (Figure 4; Wilcoxon tests, all $p > .05$).

The most abundant habitat type within pika family ranges was sedge meadow, which accounted for an average of 84% of range areas (Table 1). Although the two types of depressions in the sedge meadow habitat were roughly equal in area within pika family ranges, edges with the small depressions (which contained grasses and forbs) were more extensive than those with the more continuous "black sands" habitat. Both depression habitats represented an organic deterioration of the sedge meadow. Entrances into the family burrow system constituted 66% of holes available to pikas, and each family contained an average of about 58 burrow openings and 29 "duck holes" per pika. Mean slope score of the grid cells within family ranges averaged 1.49 (range of family means = 1.00–2.75), reflecting the primarily flat or gently sloping habitat.

We compared family ranges from which dispersing juvenile male and female pikas emigrated, to which they immigrated, and family ranges where juvenile pikas were philopatric, from 1990 to 1991. Comparisons were made for both the habitat in range areas occupied by families (Table 1) and for the amount of range area per individual within pika families, both on a total range and per grid cell basis. Because eight habitat characteristics were examined, statistical acceptance was set at $\alpha' = 0.0064$. In fact, however, 192 statistical tests were run with both parametric and nonparametric procedures. None of the family ranges of dispersing and philopatric pikas exhibited significant differences in any of the habitat characteristics.

Both males and females, however, exhibited a tendency to disperse from family ranges that had a high density of burrows

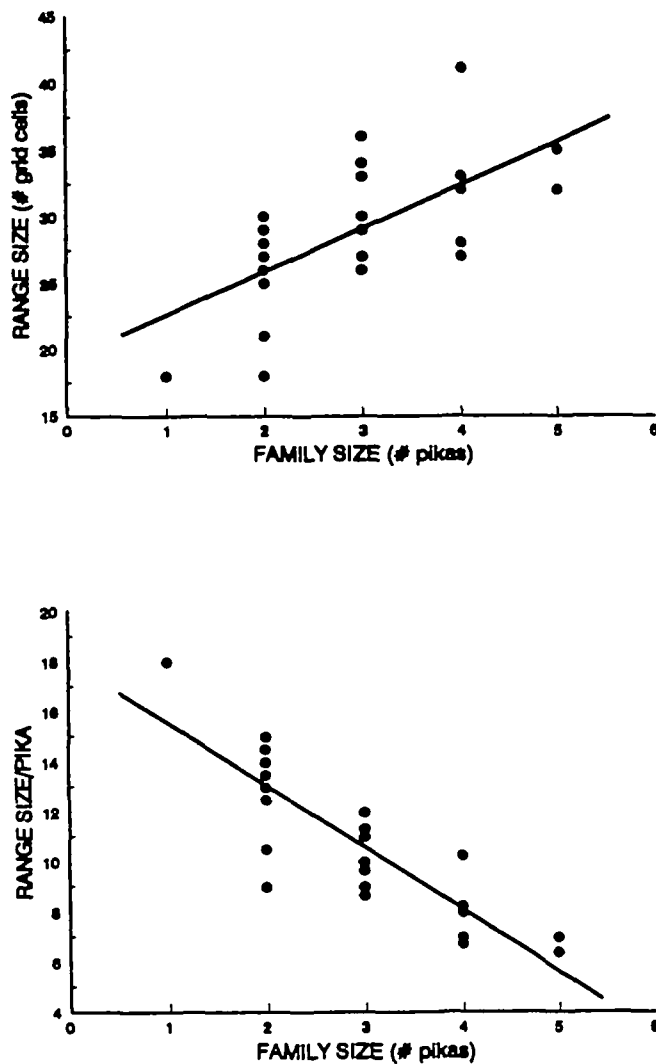


Figure 3
Range size in number of 5×5 m grid cells for pika families of different sizes (top), and range size per pika for pika families of different sizes (bottom). Least squares linear regression lines are shown, statistics are given in the text.

to families with a lower density of burrows. Males emigrated from ranges with an average of 6.09 burrows/grid cell and immigrated to ranges with an average of 5.25 burrows/grid cell (Wilcoxon test, $n = 18, 12, z = 1.77, p = .08$). Females emigrated from ranges with 6.38 burrows/grid cell and immigrated to ranges with 5.34 burrows/grid cell (Wilcoxon test, $n = 9, 8, z = 1.88, p = .06$). In addition, females exhibited a slight tendency to disperse toward sloping parts of the habitat [emigrating from slope scores of mean = 1.22, and immigrating to slope scores of mean = 1.56 (Wilcoxon test; $n = 9, 8; z = 2.17; p = .03$)]. Although these tendencies might well have occurred by chance, we present them because among all tests run, they represented the strongest patterns of potential influence of habitat on pika dispersal.

Membership of pika families

In 1991, 30 pika families contained an average of 2.9 adults (1.2 males and 1.7 females). We determined the composition that families might have had if no dispersal occurred between 1990 and 1991 (assuming that surviving pikas never left their

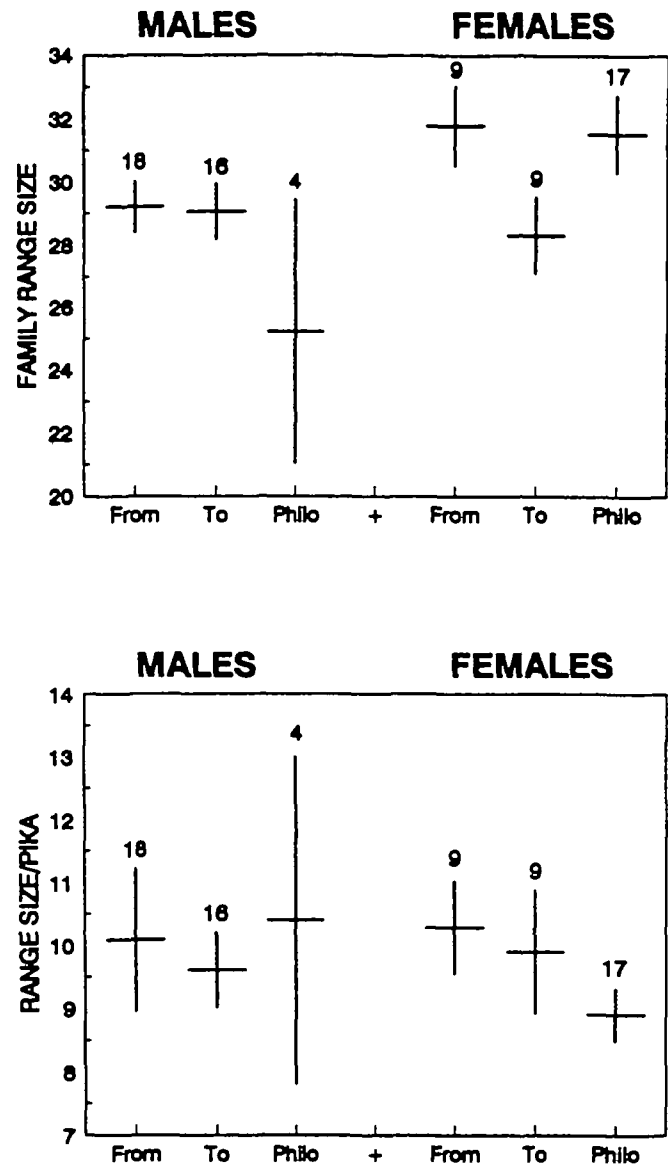


Figure 4
Family range size (top, ± 1 SE) and range size per pika (bottom, ± 1 SE) in 1991 for families from which natal dispersers emigrated ("From"), to which natal dispersers immigrated ("To"), and families with natal philopatry ("Philo"). Males are shown on the left and females on the right. Numbers above the lines indicate sample sizes.

Table 1

Mean, standard error, and range of 7 habitat characteristics of 26 pika family ranges

Characteristic	Mean	SE	Minimum	Maximum
Sedge meadow	606 m ²	34 m ²	85	889
Small depressions	58 m ²	4 m ²	34	125
Black sands	59 m ²	14 m ²	0	302
Edges with				
small depressions	539 m	35 m	167	960
black sands	147 m	25 m	0	394
Burrows	156	10	72	270
Duck holes	79	5	36	170

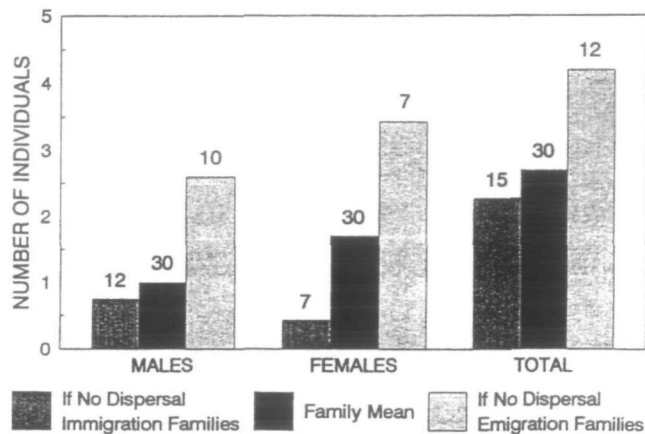


Figure 5
Numbers of males, females, and total pikas in pika families in 1991 (solid bars). To the left of the solid bars are the numbers of individuals that families which received immigrants would have had if there had been no dispersal ("immigration families"). To the right of the solid bars are the numbers of individuals that families which produced emigrants would have had if there had been no dispersal ("emigration families"). Numbers above the bars indicate sample sizes. Statistical comparisons are given in the text.

original families and that no pikas immigrated). Families that received immigrants would have been smaller had there been no dispersal, compared to the actual composition of families, but the difference was significant only for females (Wilcoxon test; $n = 30, 7; z = 3.55; p = .0004$). For those families that produced emigrants, family size would have been significantly greater if no dispersal occurred, compared to the actual composition of families (Figure 5). This comparison was significant for males, for females, and for adults combined (respectively, Wilcoxon tests; $n = 30, 10, z = 3.16, p = .002; n = 30, 7, z = 3.60, p = .0003; n = 30, 12, z = 2.87, p = .004$).

These results on family composition are not surprising because families without immigrants would be smaller and families without emigrants leaving would be larger. Because pika families could both receive immigrants and be the source of emigrants, however, the results that emerged were not guaranteed (e.g., all families could have exhibited immigration and emigration, so that total family sizes would not change). The difference in average sizes of families that produced and received dispersers would have been large if there had been no dispersal (Figure 5). Both males and females, however, dispersed in a pattern that resulted in roughly equal average size between families that produced and received dispersers (Figure 6).

For juvenile pikas in 1990 that became adults in 1991, we divided pika families into those from which pikas emigrated, those to which pikas immigrated, and those with philopatric pikas. These categories were not independent because the same family potentially could occur in all three categories. Our procedure, however, provided a qualitative basis for comparison among types of families. Families from which juvenile males emigrated between 1990 and 1991 had significantly more females compared to the families into which these males immigrated (Figure 6; Wilcoxon test; $n = 18, 18, z = 2.62, p < .008$). The families of philopatric males were similar in numbers of males and females to those into which males emigrated. Families into which juvenile females immigrated had slightly more males and fewer females than the families of philopatric females (Figure 6; the latter comparison approached significance, Wilcoxon test; $n = 9, 18, z = 1.85; p = .06$).

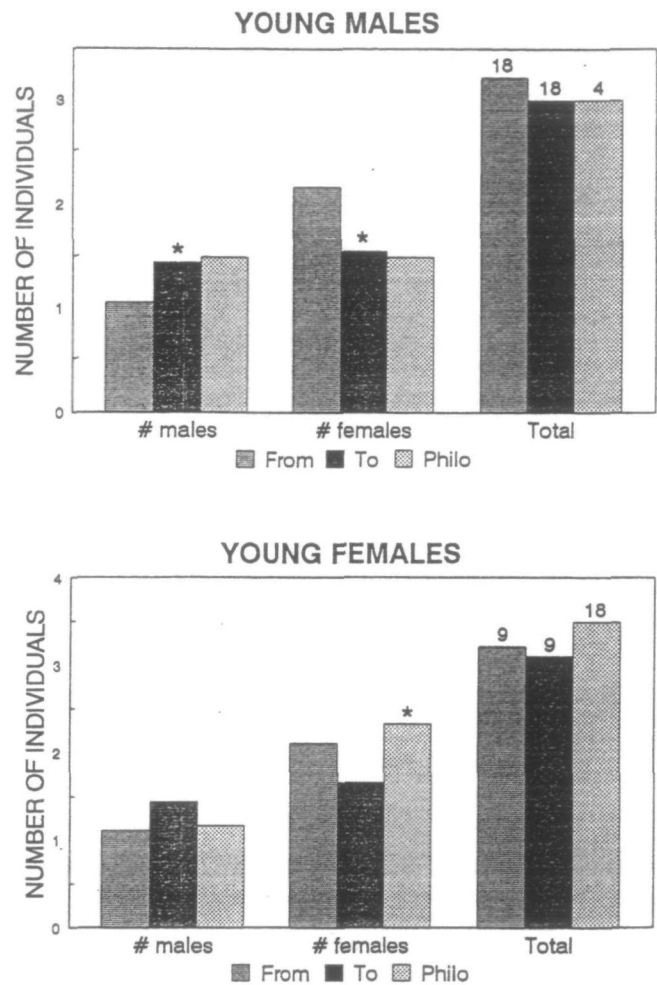


Figure 6
The number of males, females, and total pikas in families from which dispersing male (top) and female (bottom) juvenile pikas emigrated ("From"), families to which they immigrated ("To"), and families where they were philopatric ("Philo") between 1990 and 1991. Stars above bars indicate significant differences from the adjacent bar to the left (statistical comparisons in the text). Numbers above the right-hand sets of bars indicate sample sizes.

Sex ratio within pika families in 1991 varied more strongly among the different types of pika families than did the overall number of males and females. For juvenile pikas in 1990 that became adults in 1991, families from which males emigrated had significantly more females per male than families into which males immigrated or where males were philopatric (Figure 7; Wilcoxon tests; $n = 16, 18, z = 2.85, p = .004; n = 16, 4, z = 2.66, p = .008$, respectively). Also, the number of males per female in families into which females immigrated was higher than in either the families from which they emigrated or the families of philopatric females, although this was only significant in the latter comparison (Wilcoxon tests; $n = 9, 9, z = 1.86, p = .06; n = 9, 18, z = 2.10, p = .04$, respectively).

To examine why juvenile females dispersed to families with more males per female, we examined the ratio of males to females in families in 1990 and the number of young per female from these families that survived to adult age in 1991. Success at producing surviving offspring per female was significantly associated with the sex ratio of males to females in families (Figure 8; Spearman's $r = .371, df = 28, p = .04$). Also, the number of males in these families was significantly

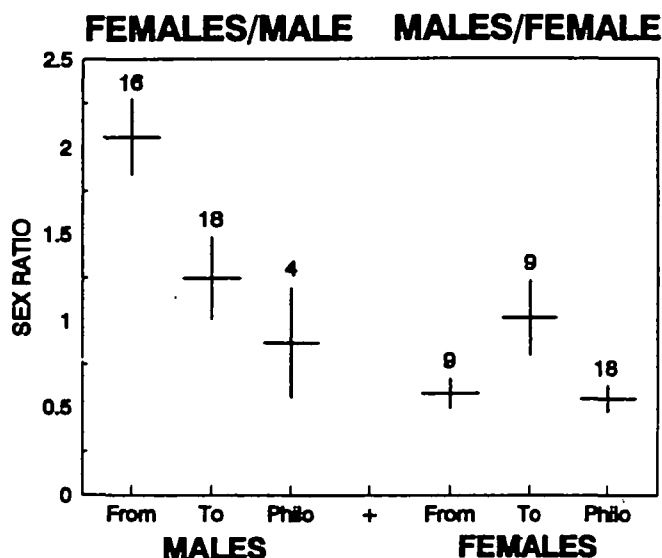


Figure 7

Sex ratio (± 1 SE) in number of females per male (for males, on the left) and number of males per female (for females, on the right) in pika families from which juvenile pikas emigrated ("From"), families to which they immigrated ("To"), and families where they were philopatric ("Philo") between 1990 and 1991. Numbers above the bars indicate sample sizes. Statistical comparisons are given in the text.

associated with the total success of families at producing surviving offspring (Spearman's $r = .385$, $df = 28$, $p = .04$), but a similar association was not evident for the number of females in families (Spearman's $r = .178$, $df = 28$, $p = .35$).

The role of kinship

To examine possible influences of kinship on patterns of dispersal and philopatry, we examined cases where putative relatives (full or half-sibling and parent-offspring relationships only) resided in families as yearling adults in 1991. Yearling males that had remained philopatric were no more likely to have a male relative present in their family than were dispersing males (Figure 9). However, philopatric yearling males were significantly more likely to have a female relative present in their family in 1991 than males that dispersed to new families. In addition, males that dispersed left female relatives behind, as in all known cases these males would have had a female relative present in their family had they not dispersed. Even though only philopatric yearling females had related males in their families, these females were no more likely to have a male relative in their family than juvenile females that dispersed to new families (Figure 9). Philopatric yearling females, however, were significantly more likely to have female relatives present in their families than females that dispersed.

In three cases, pairs of male siblings that were born in 1990 dispersed together to new families in 1991. In one case, a pair of young sisters dispersed to an adjacent family. Two adult males that changed families between 1990 and 1991 moved away from daughters that could have been their offspring, but two additional adult males that were philopatric had potential daughters in their families. In none of the cases of dispersal, however, did dispersal bring opposite-sex relatives together. Rather, close relatives of the opposite sex occurred in the same family only when males and females were philopatric.

Our indirect assessments of kinship are contingent on the mating history within families. There is strong behavioral evidence that most effective matings occur within rather than

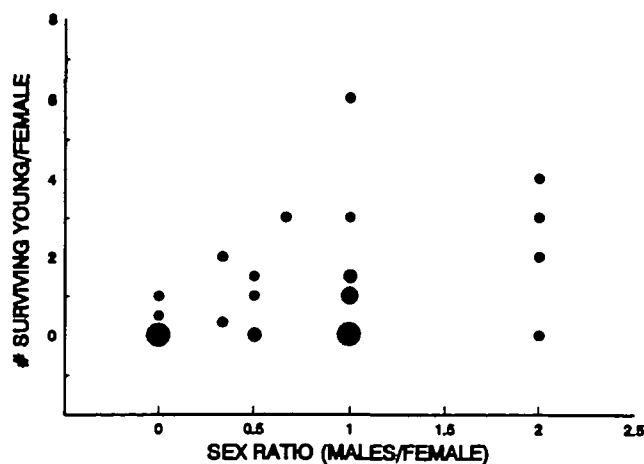


Figure 8

Number of juvenile pikas (from 1990) that survived to 1991 per mother in 1990 for 30 pika families, plotted against the adult sex ratio (in males per female) of these families in 1990. The size of the dots show ties: small, $n = 1$; medium, $n = 2$; large, $n = 3$; extra large, $n = 5$. Correlation coefficients are in the text.

between families, although there appears to be variability among different mating system types. Of 171 observed mating attempts, 87% were between adults occupying the same family home range. The ability of males to mate guard females appeared contingent on the sex ratio within the family, with males in monogamous and polyandrous families being more successful at warding off trespassing males from outside the family than males from polygynous families. Of the 22 instances where males attempted to mate with females from other families, only 2 instances (9%) occurred within monogamous families and none within polyandrous families. Not only were males effective at chasing off trespassing males, but females actively rejected mating attempts by some nonfamily males (Smith and Wang, 1991). Further, in a 4-year study of a fully marked population of plateau pikas, matings occurred at the activity centers of the estrous female, and in no instances were any courtship behaviors or normal copulatory behaviors executed by trespassing males (Wang, 1990). Thus, in the absence of genetic evidence, it appears that most successful matings occur between adults of the same family.

DISCUSSION

Plateau pika dispersal and philopatry

The extremely short natal and adult dispersal distances of the plateau pika and the predominant philopatry between years of most individuals are unusual among mammalian species (Figures 1 and 2). Pikas that disperse move only a few family ranges from where they were born, and juvenile males appear to be the predominant dispersers. Thus, although plateau pikas resemble American pikas (*O. princeps*) in being highly philopatric, they differ in that the latter do not exhibit a male-biased natal dispersal pattern (Smith, 1987; Smith and Ivins, 1983). Distances moved by dispersing pikas were extremely short and similar to philopatric banner-tailed kangaroo rats (*Dipodomys spectabilis*), although little or no sex bias occurs in the natal dispersal of kangaroo rats (Jones, 1987). Thus, plateau pikas exhibited the male-biased natal dispersal that is common among mammalian species (Dobson, 1982; Greenwood, 1980) and also the extremely restrictive dispersal movements exhibited by American pikas and banner-tailed kangaroo rats.

		MALE RELATIVE		P			MALE RELATIVE		P
		present	absent		present	absent			
MALES	philopatric	0	2	0.48	FEMALES	philopatric	4	14	0.29
	dispersed	6	12			dispersed	0	6	
	IF philopatric	8	11	0.71		IF philopatric	3	4	0.12
		FEMALE RELATIVE		P			FEMALE RELATIVE		P
		present	absent		present	absent			
MALES	philopatric	3	1	0.002	FEMALES	philopatric	11	2	0.006
	dispersed	0	19			dispersed	2	7	
	IF philopatric	18	0	< 0.001		IF philopatric	8	0	0.002

Figure 9

Presence or absence of putative male and female relatives ($r = .25$ or $.50$, see text) for juvenile male and female pikas that were philopatric or that dispersed to new families between 1990 and 1991. "If philopatric" indicates family composition in the natal family which juvenile dispersers might have experienced if no dispersal had occurred. Probability levels are from Fisher's Exact tests for 2×2 contingency tables.

Competition for environmental resources

The hypothesis that successful dispersers benefit from increased access to environmental resources in their new home area has considerable support from studies of mammals, particularly with respect to natal dispersal of females (e.g., Dobson, 1979, 1981, 1982; Dobson and Jones, 1985; Moore and Ali, 1984). In plateau pikas, larger families were associated with larger family ranges (Figure 3), but also with less habitat area per pika. Thus, if dispersal were to yield a benefit of decreased competition for environmental resources in the new family, pikas should have been observed to move from large families to smaller ones.

In support of this prediction, natal dispersal of plateau pikas resulted in an equalization of local density of pika family members (Figure 6). Dispersal favored both males and females from larger families, that would have had high densities in the absence of dispersal (Figure 5). Dispersers, especially females, moved to families that would have been smaller if dispersal had not occurred. Families to which juvenile females immigrated had slightly smaller ranges (although not significantly) than the families from which these females emigrated, but available range area per pika did not differ between these two types of families (Figure 4).

Evidence that competition for resources was a factor promoting natal dispersal does not, however, indicate the potential benefits of specific environmental features, only that they were likely related to local population density. We expected our habitat measures (Table 1) to have considerable influence on pika biology and to demonstrate specific benefits accruing to dispersers. The mosaic of microhabitat types should influence the number and types of food resources available to pikas. Pikas frequently forage along the edge of the sedge hab-

itat, perhaps to gain shelter from abundant avian predators. Such edges also contain many burrow entrances, an important resource when a predator appears. Finally, parts of the habitat that have greater slope (i.e., are hilly) restrict the vision of pikas (allowing closer approaches by predators) and may have a different cycle of plant growth due to their relative dryness. In fact, however, there were no differences in characteristics of the habitats from which or to which pikas dispersed. These analyses suggest that none of the habitat factors that we measured exerted individual influences on dispersal patterns, although we cannot rule out their potential cumulative effect.

Our failure to identify benefits to dispersers of specific habitat features suggests that the environment may be relatively uniform to plateau pikas (Smith and Wang, 1991), and concomitantly that habitat uniformity might limit the benefits of dispersal or increase the costs of long-distance dispersal. All mammalian and avian predators in the region hunt over a scale much larger than the size of family territories of plateau pikas. Long-distance dispersal may increase predation risk, while the similarity of most territories may provide equivalent protection from predators. We also have evidence that specific territories varied widely in family composition and size among years; only 15% (4/26) of all territories contained the same mating system type between 1990 and 1991 (Dobson et al., unpublished data). Thus, it did not appear that specific habitat features determined where an animal dispersed; only local density was a determinant. There was sufficient variability in number of overwintering animals in families within a short radius (due to stochastic effects of mortality) to allow for dispersal to equalize density, but perhaps insufficient benefits and increased costs inhibited long-distance dispersal movements.

Competition for mates

The hypothesis that successful dispersers benefit from increased access to mates or mating opportunities in their new home area also has considerable support among mammalian species, particularly with respect to natal dispersal of males (e.g., Dobson, 1982; Dobson and Jones, 1985; Moore and Ali, 1984). Plateau pikas are an ideal species for examining the costs and benefits to dispersers of the competition for mates hypothesis because they simultaneously exhibit a variety of mating combinations (monogamy, polyandry, polygyny, promiscuity) among families (Liang, 1981; Smith et al., 1986; Smith and Wang, 1991; Wang and Dai, 1990; Wang and Smith, 1989). If competition for mating opportunities influenced natal dispersal of either males or females, then pikas should have dispersed from families with fewer members of the opposite sex to families with more members of the opposite sex.

Juvenile males dispersed from families that, on average, had higher numbers of females to families with significantly fewer potential mates (Figure 6). This pattern is the opposite of that predicted by the competition for mates hypothesis. In addition, the families that emigrating juvenile males left behind had significantly fewer males than the families in which they settled (although this pattern undoubtedly results from the transfer of the dispersing male himself). When these patterns are combined, however, the conclusion is clear: juvenile males leave behind families that contain more potential mates per male and settle in families with fewer potential mates (Figure 7). Although more subtle influences of competition for mates are possible, the results strongly suggest that competition for mates is not a major influence on the natal dispersal of males.

Juvenile females dispersed from families with relatively low numbers of males and high numbers of females, on average, to families with slightly more potential mates and fewer females, but these differences were not significant (Figure 6). Considered together, however, natal dispersal of females resulted in a shift from families with lower numbers of males per female to families with higher numbers of potential mates per female (Figure 7). Thus, by dispersing, juvenile females might have gained increased access to male mates.

Our behavioral data indicate that the potential costs and benefits of dispersal in relation to family composition may be more complicated than just the numerical abundance of potential mates. All females entering the breeding season became pregnant; and in families with multiple males there was no evidence of mate choice. Females in estrus were often observed to mate alternately and repeatedly with all males in their family (Dobson et al., unpublished data). Thus, we cannot demonstrate costs or benefits, either quantitatively (percent pregnant) or qualitatively (increased opportunity for mate choice within families) for females that moved to families with larger number of males.

For males, the issue appeared to center on their ability to successfully mate guard estrous females within their families. In this and a previous study (Smith and Wang, 1991), males in polygynous families were more likely to be cuckolded from outside the family than males in monogamous or polyandrous families. Polygynous males apparently have difficulty simultaneously mate guarding multiple females. Males, therefore, may increase certainty of paternity by teaming with a second breeding-age male in a family, rather than risk increased cuckoldry by unknown trespassing males. From another perspective, males from multimale families may also be more free to roam and solicit extra-familial matings than a solitary polygynous male trying to defend multiple females. Thus, with regard to certainty of paternity, dispersing males might benefit from movements into families with other males and away from families with multiple females.

An alternative hypothesis is that both males and females dispersed to families with more males because of the high levels of paternal care that they provide (Smith and Wang, 1991). Adult males interact amicably with recently weaned juveniles, generally interact more frequently than adult females with the young pikas, and sometimes care for offspring that they have not fathered (Smith et al., 1986; Smith and Wang, 1991). If such benefits were substantial, then we would expect increased levels of paternal care to result in increased survival of juveniles to reproductive age. This prediction was supported by the significant association of number of surviving young per adult female with the number of males per female within pika families (Figure 8).

One other possible social advantage for some pikas undergoing natal dispersal was cooperation with a same-sex relative. Three pairs of full or half-brothers and one pair of sisters dispersed to a new family together. Co-dispersal of brothers occurs in some social carnivore species (e.g., Bygott et al., 1979; Pusey and Packer, 1987; Rood, 1987; Waser et al., 1994), but similar patterns have not been reported for smaller mammals such as rodents and lagomorphs.

We conclude that there is little evidence that competition for mating opportunities influences natal dispersal of males or females. However, competition for resources in the social environment, particularly male care of juvenile offspring, may have been an important influence on the natal dispersal of both genders.

Inbreeding avoidance

The idea that avoidance of incestuous mating might influence natal dispersal is controversial. Shields (1987, 1993) has argued that inbreeding is beneficial to individuals, and thus could hardly be an important influence on dispersal patterns. Alternatively, considerable evidence from captive animals indicates inbreeding depression from incestuous matings (e.g., Lacy et al., 1993; Ralls et al., 1979), and attempts have been made to find such evidence in the field (e.g., Alberts and Altmann, 1995; Hoogland, 1995; Keane et al., 1996; Ralls et al., 1986). Although inbreeding (mating between genetic relatives) occurs in virtually all populations of sexual, diploid animals, natal dispersal patterns can be very effective in minimizing the rate of inbreeding (Dobson et al., 1997; Sugg et al., 1996). Smith (1993) indicated that the plateau pika is a prime candidate for high levels of inbreeding, due to the extreme philopatry it exhibits. Thus, it is reasonable to consider indirect evidence concerning the influence of inbreeding minimization on natal dispersal.

We examined the prediction that if inbreeding influenced natal dispersal, then movements should be away from close relatives that are potential mates and into families of distantly related individuals. Although philopatric males usually had a close female relative present in their families, the sample was only four males. Nonetheless, dispersing males did not have female relatives present in their new families, a significant difference from the philopatric males and from what dispersing males would have faced had they stayed in the natal family (Figure 9). Due to the more substantial natal dispersal of males, philopatric females seldom had closely related males in their families, and dispersing females did not settle with close male relatives. For both males and females, four cases of co-dispersal of pairs of siblings contained only same-sex individuals. In only one case did natal philopatry of a male and female result in a monogamous family, and the reproductive success of this family was not known. In conclusion, we cannot rule out an influence of inbreeding minimization on the natal dispersal of males or females, but further evidence with genetic markers is needed for a direct test of this hypothesis.

Philopatry

Philopatry has received far less research attention than dispersal behavior, perhaps because it is more difficult to discern influences on the lack of movement (Waser and Jones, 1983). In many mammalian species, it is the females that are most philopatric (Dobson, 1982; Greenwood, 1980). Plateau pikas reflect that pattern, although they are somewhat unusual among mammals in that both males and females may be philopatric. Possible evolutionary advantages to philopatry include avoidance of dispersal through unfamiliar habitat and the associated risk of predation, advantageous resource conditions in a familiar natal habitat, cooperation with other individuals such as close kin, and the presence of a proven successful breeding situation. For the plateau pika, dispersal does not occur over unfamiliar habitat. Rather, exploration of possible new family ranges can occur with just a few minutes or less of locomotion, and the new family range of most of the dispersers was easily visible from the natal range. Thus, the observed short-distance dispersal of the plateau pikas may not have been associated with a dramatic increase in the risk of predation, but long distance movements may have been costly due to the intense predator activity in the habitat.

While natal dispersal resulted in an equalization in local density among pika families (Figure 5), philopatric individuals were associated with families that already contained similar numbers of individuals to the families in which dispersers settled (Figure 6). Philopatric females lived in families that contained significantly more females than the families to which dispersing females moved, but they also lived with slightly fewer males, so that the total family size was not significantly different from that for dispersing females. Thus, without dispersing, philopatric males and females ended up in "average" families with respect to available habitat resources. Of course, philopatric individuals did not have to expend time and energy to learn the idiosyncrasies of a new range, but such costs would be difficult to quantify without specific behavioral and energetic experiments.

Philopatric females apparently did not benefit from the presence of high numbers of males per female to assist with the parental care of their young (Figure 7). Rather, a lower amount of paternal care for young might be a cost of philopatry. Philopatric females, however, were much more likely to have close female relatives present in their families than dispersing females (Figure 9). In behavioral interactions with recently emerged juveniles that are not their own offspring, adult females exhibit similar "parental" attention as that of adult males, and these females are more likely to utter alarm calls when predators are sighted than adult males (Smith and Wang 1991; Smith et al., 1986). Such "aunting" behavior has not previously been described in small mammals. If aunting behavior characterized related females, as we suspected but could not document, then the presence of related females might provide a reproductive resource for philopatric mothers.

Conclusion

Populations and species of animals exhibit a diverse array of patterns of philopatry and dispersal. Among mammalian species, however, the predominant pattern of natal dispersal is for males to disperse and females to remain philopatric (Dobson, 1982; Greenwood, 1980; Waser and Jones, 1983). The usual interpretation of this pattern is that male natal dispersal is predominantly influenced by either competition for mates or by the minimization of inbreeding, and that natal philopatry by females primarily results from advantages in competition for environmental resources (e.g., Dobson, 1979, 1981,

1982; Dobson and Jones, 1985; Moore and Ali, 1984; Smith, 1993). We analyzed the respective costs and benefits of the observed pattern of dispersal in plateau pikas. The relative uniformity of the habitat and variety of different combinations of adults within nearby families has led to a pattern of predominantly philopatric settlement or short dispersal movements; long dispersal movements might only be associated with high costs and no known additional benefits. Natal dispersal of both male and female plateau pikas appeared to minimize the potential costs of competition for environmental resources within local family ranges. In addition, females moved to families with more males per female than their original families, thus benefiting from the high levels of male care for offspring. There was no evidence that dispersal was driven by competition for mating opportunities. Natal philopatry, expressed most often by females, may be influenced by resource competition through beneficial conditions of local family densities and the social resource of having closely related adult females present. Thus, dispersal movements of plateau pikas demonstrate the interplay of environmental and social influences on both males and females.

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