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## The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation

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**Abstract** Habitat fragmentation is becoming increasingly common, yet, the effect of habitat spatial structure on population dynamics remains undetermined for most species. Populations of a single species found in fragmented and nonfragmented habitat present a rare opportunity to examine the effect of habitat spatial structure on population dynamics. This study investigates the impact of highly fragmented habitat on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) population with a mainland-island spatial structure. Juvenile dispersal patterns in fragmented habitat revealed that individuals tended to disperse to neighboring habitat patches. However, within-patch band-sharing scores from multilocus DNA fingerprints did not differ from what would be expected if individuals were assorting randomly among habitat patches each year. Multiple, short-distance dispersal targets for juveniles and occasional long-distance dispersal events suggest that habitat fragmentation on this scale has not resulted in restricted dispersal and a genetically subdivided population. Although pikas tended to mate with the closest available partner, DNA fingerprinting band-sharing scores between mated pairs were consistent with a random mating hypothesis. Random mating in this population appears to be an incidental effect of dispersal in a fragmented habitat. This pattern is distinct from that found in nonfragmented habitat (large talus patches) where mating was non-random and consistent with mating between individuals of intermediate relatedness. DNA fingerprinting data revealed within-species variation in the mating habits of the pika directly attributable to habitat spatial structure.

**Key words** Habitat spatial structure · Dispersal patterns · Mating behavior · Multilocus DNA fingerprinting · Metapopulation

### Introduction

The effect of habitat fragmentation on population dynamics depends upon the nature of the fragmentation and the life-history characteristics of the species concerned (Wilcox and Murphy 1985; Gilpin and Soulé 1986; Soulé 1986; Gilpin 1991; Hanski and Gilpin 1991; Wu and Levins 1993; Lacy and Lindenmayer 1995). Populations found in fragmented habitat may act as metapopulations, a collection of local populations connected via dispersal (Levins 1969, 1970). There is little information on the dynamics of naturally occurring metapopulations, for instance on dispersal rates between and patterns of turnover among local populations (Harrison 1991). Restricted dispersal can result in increased levels of inbreeding, smaller effective population sizes and loss of genetic variation (Gilpin 1991; Hastings and Harrison 1994; Lacy and Lindenmayer 1995). Important variables that may influence dispersal rate, and ultimately population stability and persistence, include the number of habitat patches, and their size and spatial configuration (den Boer 1979; Ebenhard 1991; Hansson 1991; Wu et al. 1993).

Harrison (1991) outlines four types of metapopulations, each with different impacts on population dynamics: (1) classic or true metapopulations; (2) mainland-island systems; (3) patchy populations; and (4) non-equilibrium metapopulations. A classic metapopulation consists of habitat patches of equal size. These metapopulations persist through a balance between extinction and recolonization of habitat patches (Hanski 1991). Simulation of population dynamics in a hypothetical three-patch classic metapopulation resulted in a precipitous drop in heterozygosity (Gilpin 1991). However, because very few metapopulations exhibit extremely low levels of heterozygosity, classic metapopulations are probably un-

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common (Gilpin 1991). Mainland-island systems defined by large habitat patches and many small patches are more common (Harrison 1991). Regional stability is unaffected by local extinctions in the smaller patches because the extinction-resistant mainland acts as the major provider of colonists for the extirpated patches (Ebenhard 1991). Genetic variation, in turn, is maintained in the mainland population because of its size. Patchy populations are pseudo-metapopulations. Although distributed over patchy or spatio-temporally variable habitat, frequent movement between patches effectively prevents local extinctions and promotes panmixis in these populations (Harrison 1991). Intermediate cases are found which involve both mainland-island dynamics and patchy population dynamics (Ebenhard 1988). The spatial arrangement of patches promotes frequent dispersal among proximate patches that form a type of mainland with the more distant patches acting as islands in a mainland-island sense. Non-equilibrium metapopulations represent declining populations in which subpopulations in habitat patches go extinct and patches are not recolonized (Harrison 1991).

Many empirical questions about metapopulation dynamics remain unanswered. The limits of the existing empirical evidence prevent broad generalizations about the dynamics of metapopulations with differing spatial structure. Within-species comparisons of populations found in both continuous and fragmented habitats are of particular value. These comparisons allow the impact of habitat spatial structure on population dynamics to be assessed within one species with specific life-history characteristics.

Pikas (*Ochotona princeps*) represent a model system for such a comparison. The pika, a small alpine lagomorph (~150 g), occurs in talus habitats throughout western North America (Smith and Weston 1990). Talus habitat can be large continuous or semi-continuous patches ( $n = 100$  individuals) as well as highly fragmented habitat with small patches ( $n = 10$ ) connected via dispersal. Adult pikas are individually territorial and rarely disperse (Barash 1973; Tapper 1973; Smith and Ivins 1983). Territories are identifiable by the presence of one or two large haypiles. Haypiles, constructed by the resident adult, are stores of vegetation that serve as a food source during the winter months (Smith and Ivins 1983). Juveniles typically obtain a territory during the summer of their birth and tend to settle on the first available territory (Smith 1987; Peacock 1997). However, genetic analysis of populations separated by 2–10 km of semi-continuous talus habitat suggest that gene flow occurs in each generation (Hafner and Sullivan 1995; Peacock 1997). DNA fingerprinting band-sharing scores between mated pairs in a population found in continuous habitat suggest that mating was non-random and individuals chose mates of intermediate relatedness (Peacock and Smith 1997).

This study was undertaken to: (1) assess the impact of highly fragmented habitat on the dispersal patterns and mating habits of pikas and (2) evaluate the dynamics of a population with a mainland-island spatial structure. We

examined: (1) dispersal patterns of juvenile animals, including dispersal distance and location compared with territory availability, (2) the spatial arrangement of mated pairs (same island or neighboring islands) in relation to DNA fingerprinting band-sharing scores between mated pairs, (3) the pattern of relatedness of pikas across the population, and (4) average heterozygosity ( $H$ ) of populations found in continuous and fragmented habitat types.

## Materials and methods

### Study site

This study was conducted at Bodie, Mono County, California, United States (May–July, 1988–1991). The Bodie site (mean elevation = 2550 m) consists of approximately 100 talus islands of various sizes formed from the tailings of abandoned gold mines. The talus islands were colonized around 1900 and support from 2 to ~50 animals (Severaid 1955; Peacock 1997). Pikas have been found on 81 of the 100 islands (Smith 1974a). The islands are separated from each other by Great Basin northern desert shrub, primarily sagebrush and bitterbrush. Pikas colonized the Bodie Hills from the Sierra Nevada, 35 km away via natural rock outcrops scattered throughout this plateau sometime during the Pleistocene (Smith 1974a). The habitat at Bodie is typically unsaturated (up to 40% of the islands can be unoccupied), unlike sites at higher and cooler elevations (Smith 1974a). Sites such as Bodie with high diurnal temperatures during the summer months mark the distributional boundary of pika populations along the eastern Sierra Nevada (Smith 1974a, b). Juveniles dispersing between islands are at risk from predation and exposure (Smith 1974a; Ivins and Smith 1983). In 1989 the population began to decline. In 1991, populations in 81% of the occupied islands in the south had gone extinct.

Sixteen islands and a mainland area (High Peak) in the north half of the study area were included in the study (area 100 ha, 1.0 km reach; Fig. 1). The High Peak mainland consists of many interconnected talus patches (each patch <15 m from its nearest neighbor). The mainland supports the largest subpopulation of pikas in this population (~50 individuals). Ground surveys and an aerial photograph of the north of the study area were used to measure the distance between and spatial configuration of the islands. A part of the High Peak mainland was trapped in all years. Islands 1–16 were trapped in 1990 and 1991 (island 10 was trapped in 1991 only).

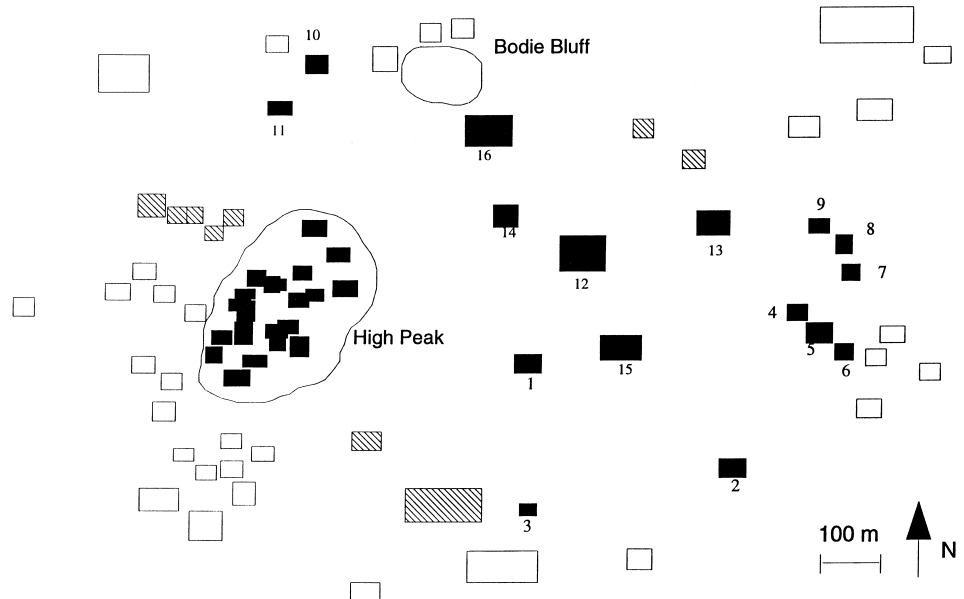
### Study population

Pikas trapped during the study were partially anesthetized with an inhalant anesthetic (Metofane), weighed, sexed and given colored ear tags for individual identification. Ear tissue was collected for genetic analysis during the tagging procedure. Adults were defined as residents on an island if they were observed haying and/or if >>75% of all independent observations of the animal occurred on that island. Observations were made during active periods, 0700–0900 hours and 1600–1930 hours, and observation sites were rotated each 0.5 h. Each island was observed for a similar period each field season (12 h,  $SD \pm 5.27$ ). Continuous scan sampling (Altmann 1974) was used to record all independent movements of each unambiguously identified animal during an observation period. The maximum number of adults an island could support was based upon a combination of census data spanning 1972–1991 and published home range data (Smith 1987; A. T. Smith, personal communication).

### DNA fingerprinting

Total genomic DNA was extracted from ear tissue using a CsCl-EB (ethidium bromide) ultracentrifugation gradient method (Dow-

**Fig. 1** Map of the study site. The *squares* represent talus islands in the north half of the Bodie population and the sizes are proportional to the area. The *black squares* are the talus islands included in the study on which all adults residents were trapped and marked in 1990 and/or 1991. The *shaded squares* are islands on which only some of the adult residents were trapped. The *open squares* are islands that were periodically inspected for marked animals during the study



ling et al. 1990). DNA from each animal (7  $\mu$ g, digested with the restriction enzyme *Hin*FI) and 50 ng each of lambda DNA cut with *Hin*DIII and a *Hin*DIII-*Eco*RI double digest were loaded onto 1% horizontal agarose gels. Electrophoresis was carried out at 35 V for 48 h with recirculation of buffer (1X TAE; 40 mM Tris, 20 mM acetic acid, 1 mM EDTA). DNA was transferred overnight onto Nytran nylon membrane. We used a nonradioactive, chemiluminescent hybridization procedure (B. Hoagland and J. Bevan, unpublished work; Cate et al. 1991; Martin et al. 1991; Southern Light, Tropix, Inc.). The probe was a single-stranded oligonucleotide (Molecular Biosystems) with a sequence analogous to the 33.15 minisatellite probe (Jeffreys et al. 1985a, b). Membranes were stripped and reprobed with radiolabelled lambda to visualize the in-lane lambda size standard fragments. In preliminary analyses, the alkaline phosphatase labelled probe did not hybridize to the lambda size standard, so in-lane size standards were used to facilitate gel-wide pairwise comparisons.

The lambda size standard films were overlaid onto the chemiluminescence-generated images for scoring. DNA from the same control individual was run in multiple lanes on each gel. The migration pattern of the control bands was highly correlated with the migration pattern of the lambda size standard fragments both within and between gels ( $r^2 = 0.985$ ; Peacock 1997). Bands were considered the same if the overall band intensity was not less than half (Westneat 1990) and if they were the same distance from the nearest in-lane size standard fragment. The proportion of bands shared ( $D$ ) was calculated as twice the number of shared bands ( $N_{AB}$ ) over the total number of bands in both individuals [ $D = 2N_{AB}/(N_A + N_B)$ ] (Wetton et al. 1987; Westneat 1990; Lynch 1991; Piper and Rabenold 1992). All resolvable bands between 21 and 2 kb were scored.

#### Parentage determination

Mothers were initially identified using observations of spatial overlap. DNA fingerprints of juveniles were compared to those of the adult male and female residents on the islands where the juveniles were trapped. For those cases in which both parents were not on the same island all pairwise comparisons between juveniles and resident adults on neighboring islands were conducted for those individuals with a sufficient sample of DNA. Juveniles share 50% or more of their fingerprint bands with each parent and all juvenile bands should be present in one or the other parent (Westneat 1990). However, mutation to new length variants in minisatellite regions occurs at a high rate and a small percentage of novel frag-

ments can be expected (Jeffreys et al. 1985a; Westneat 1990). Putative parents were considered the biological parents if: (1)  $D \geq 0.5$  with the juvenile, (2) juveniles had zero, one or two novel fragments, and (3) juveniles with one or two novel fragments had a sibling with zero novel fragments. Siblings were identified using a combination of: (1) spatial proximity, (2) birth dates determined using a von Bertalanffy growth curve (Millar and Zwickel 1972), (3) high band-sharing (i.e.,  $D \geq 0.5$ ) and (4) DNA fingerprinting parentage analysis. A 95% confidence interval was then calculated from the distribution of band-sharing scores between juveniles and their parents and between siblings (first-order relatives) using equations developed by Lynch (1991b; Piper and Rabenold 1992).

#### Dispersal

The resident island of the mother was considered the natal island of each juvenile. Dispersal was assessed in two ways: (1) observed movement of marked animals both within and between islands, and (2) identification of parents and offspring that were found on separate islands using multilocus DNA fingerprinting. Distances between islands were measured as straight-line distances between the two closest points on a pair of islands

#### Mating

The spacing between mother-father pairs (determined via DNA fingerprinting parentage analysis) was measured to reveal any correlation between mate choice and distance between territories. Once parentage was determined, pairings were categorized as: (1) residents of same island; (2) residents of neighboring islands; or (3) randomly assorted with respect to the configuration of islands. These data were then compared to the availability of mates.

To determine whether pikas were mating randomly or non-randomly with respect to DNA fingerprinting band-sharing scores, two comparisons were made. First, the distribution of band-sharing scores between mated pairs was compared to the distribution of band-sharing scores between all potential mates in the population. Second, band-sharing scores between mated pairs were compared to the distribution of band-sharing scores between first-order relatives (parent-offspring and sibling pairs).

Non-parametric Monte Carlo randomization tests were conducted to test for non-random pairing between males and females (Sokal and Rohlf 1981). The pool of potential mates comprised all resident males and females within and between islands for each year, pooled across years. The mean and variance of the band-

sharing scores between mated pairs were compared to the 95% confidence intervals of distributions of means and variances of randomly drawn sets (the number of mated pairs identified during the study) of band-sharing scores from the potential mates pool. The randomized distributions were created using a FORTRAN program designed to pair males and females at random. The program was designed to continue selecting individuals if no band-sharing score was available for the pair drawn. Each individual was sampled with replacement and 10,000 iterations were generated. The 95% confidence intervals were calculated as 2.5% of all observations from each tail of the distribution.

### Population structure

Band-sharing data were used to assess whether habitat fragmentation has introduced barriers to dispersal resulting in a genetically subdivided population. High diurnal temperatures and vulnerability to predation suggest that distances greater than 300 m of non-talus habitat are a dispersal barrier in this population (Smith 1974a, b; Ivins and Smith 1983). All islands included in the study had at least one neighboring island within 210 m, and most had neighbors within 100 m. To assess whether separation by >300 m acts as a dispersal barrier, an isolation-by-distance analysis was undertaken. If non-talus habitat acts as a barrier to dispersal, average band-sharing should be higher among resident adults within islands and among residents of nearest-neighbor groups than between residents of islands separated by >300 m.

Mean band-sharing between adults within islands, between resident adults within nearest neighbor island groups (closest island or islands), and between residents of islands >300 m apart was compared to population-wide band-sharing for 1990 and 1991 (years when all islands were trapped) by a series of Monte Carlo randomization tests. The distribution of population-wide band-sharing scores was generated from pairwise comparisons of adults within and between islands (including High Peak) each year then pooled across years. The mean band-sharing score within an island was compared to a distribution of means of equal-sized, randomly drawn sets (same number of scores as the island) of band-sharing scores from the population pool (10,000 iterations per island). Randomized distributions were created for each island using the FORTRAN program described earlier. A non-random assortment of individuals within an island would be supported if the mean band-sharing score within an island was outside the 95% confidence interval of the randomly generated distribution for that island. The frequency of dispersal between nearest-neighbor islands and between islands separated by >300 m was also assessed using the above procedure. The average band-sharing among residents within each of the study islands and between clusters of nearest neighbor island groups were analyzed separately for 1990 and 1991. Similar patterns in band-sharing within and between islands between years would indicate restricted dispersal.

### Mainland-island metapopulation dynamics

Genetic variation should be maintained in a mainland-island system compared to other types of metapopulations. To assess whether Bodie is a mainland-island metapopulation average heterozygosity was compared between Bodie and a pika population found in continuous habitat (Pipet Tarn; Peacock 1997). Genetic analysis suggested that there is little differentiation between Pipet Tarn and a population 2 km away (Cabin slope,  $F_{ST} = 0.105$ ; Peacock 1997). These data and an average population-wide band-sharing score that is consistent with species considered outbred show that the Pipet Tarn population is not a genetically isolated population.

Average heterozygosity was calculated using

$$H = \frac{2n}{2n-1} \left( 1 - \frac{\sum_{k=1}^A x_k^2}{\sum_{k=1}^A x_k} \right) \quad (1)$$

from Stephens et al. (1992), where  $n$  is the number of individuals included in the analysis (Bodie,  $n = 24$ ; Pipet Tarn,  $n = 18$ ),  $A$  is the number of unique scorable bands in a sample of individuals (Bodie,  $A = 72$ ; Pipet Tarn,  $A = 69$ ), and represents allele frequencies. Because each band or allele in a DNA fingerprint is effectively dominant each allele frequency ( $x_k$ ) must be estimated from the frequency of occurrence of the  $k$ th band ( $s_k$ ), where  $x_k = 1 - \sqrt{1 - s_k}$  (Stephens et al. 1992). Average heterozygosity estimates were made from gels containing a random sample of individuals chosen from each population. Sample sizes used to estimate heterozygosities for pika populations were similar to those reported for other species using multilocus DNA fingerprinting data (15–33 individuals; Stephens et al. 1992; Scribner et al. 1994).

## Results

### Spatial dynamics

A total of 1220 h were spent observing 162 animals (105 adults and 57 juveniles) during this study. On average five independent observations were recorded per adult (5.57;  $SD \pm 3.97$ ) and two per juvenile per season (2.76;  $SD \pm 2.13$ ). A total of 47 h were spent observing islands ( $n = 32$  islands) not included in the study for marked animals (see Fig. 1). Only islands in the north half of the study area were regularly searched for marked individuals each year of the study. The islands in the south half of the study area were included in population-wide censuses conducted in 1989 and 1991.

Adults rarely disperse once a territory is established (Tapper 1973; Smith and Ivins 1983). Therefore, adult turnover rate (mortality) was calculated for each island as the percentage of adults marked on that island in 1990 who were not present on that island in 1991. The average adult turnover rate for islands 1–16, trapped in 1990 and 1991 was 62.5%. For the areas of High Peak trapped consistently from 1988 to 1991, an average of 62.3% of the adults marked in one year were not present in the following year. Turnover rate was higher in this population than that reported for pika populations found in continuous habitat (37–53%; Millar and Zwickel 1972; Smith 1978; Peacock 1997). On 53% of the islands ( $n = 9$ ) at least some of the adult residents marked in 1990 were present in 1991. Of the adults trapped during this study 27% were present on the same island for more than 1 year.

### Parentage determination

Parents were identified for 34 of 57 juveniles tagged from 1988 to 1991. DNA degradation or lack of hybridization for either the juveniles or putative parents prevented parentage analysis for 7 of the 23 juveniles for whom parents could not be identified. No parental match could be made between the remaining 16 juveniles and the resident adults on the islands where they had been trapped or resident adults on neighboring islands for which comparisons could be made. However, 6 of the 16 juveniles did have band-sharing scores with at least one resident adult on the island where they had been trapped

that fell within the 95% confidence interval for first-order relatives ( $n = 82$ ; 95% confidence interval 0.533–0.722). These band-sharing scores suggest that these adults may have been first-order relatives of these juveniles. The 10 remaining juveniles were either dispersers onto the islands where they were trapped or offspring of adults that had died before the commencement of trapping.

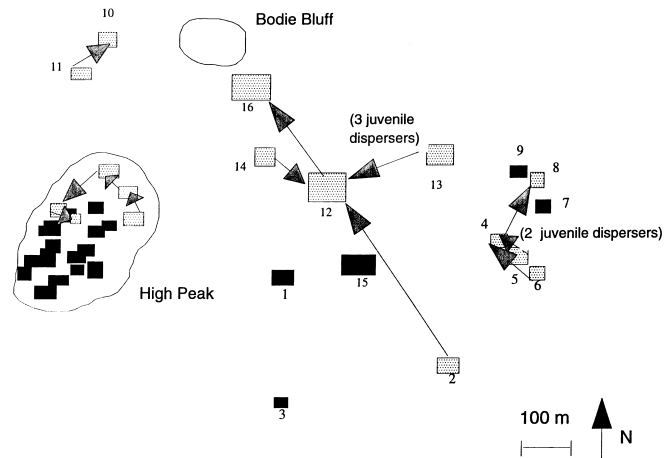
### Dispersal patterns

Altogether 15 marked juveniles and 1 marked adult dispersed during this study: 3 juveniles dispersed from their natal islands after they had been tagged, and the remaining 12 juveniles were trapped post-dispersal and their natal islands identified by the band-sharing analysis. The maximum distance a juvenile could have dispersed between islands included in the study was 1000 m. Juveniles born on High Peak that subsequently dispersed settled on territories available within High Peak ( $n = 4$ ; Fig. 2). Of the 11 juveniles that dispersed between islands, 9 left fully occupied islands (containing the maximum number of possible adult residents). Eight of the nine juveniles settled on the closest island with vacant territories. The ninth juvenile passed up four islands with available territories (three occupied, one vacant) before settling on an occupied island 396 m away. The remaining two juveniles dispersed from natal islands that had vacancies. One settled on the next closest available island and one passed up the two closest islands with available territories, settling on an island 210 m away. The average distance dispersed by juveniles (both within and between islands) was 91.25 m ( $SD \pm 72.14$ ; range 15–396). The only adult recorded dispersing moved to the nearest neighboring island (70 m).

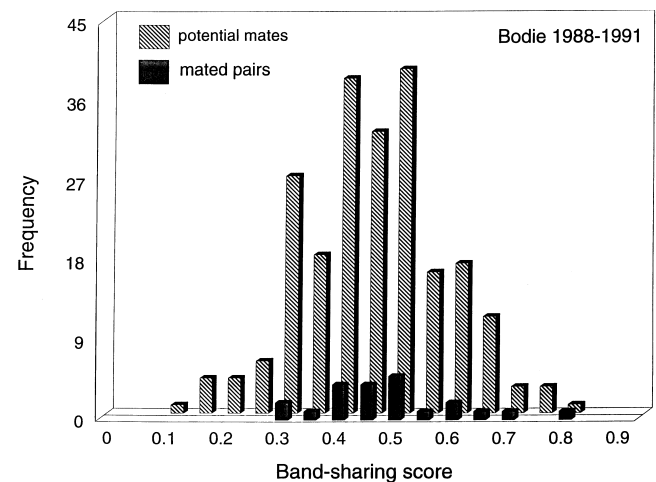
The origin of unmarked adults ( $n = 23$ ) found at the beginning of each field season on the study islands was investigated to assess the probability of marked animals dispersing to islands not included in the study. These adults were found on islands for which all residents had been marked the previous year. The unmarked adults could have been juveniles born mid-July or later and recruited onto their natal island when we were not present on the study area. Conversely, they could be dispersers from islands not included in the study. Band-sharing between these adults ( $n = 19$ ) and island residents from the previous year showed that 68% ( $n = 13$ ) had band-sharing scores with at least one adult that fell with the 95% CI for first-order relatives. These data suggest that these 13 adults were recruited onto their natal islands. The remaining 6 adults were considered dispersers from islands not included in the study.

### Mating

The 23 mated pairs identified via parentage analysis comprised 41 individuals ( $n = 23$  females;  $n = 18$  males).

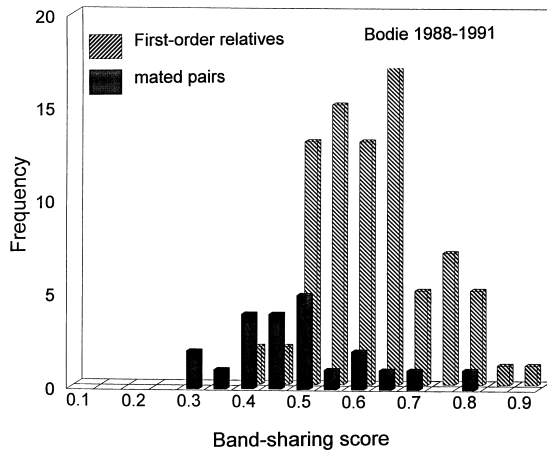


**Fig. 2** The dispersal pattern of marked juveniles ( $n = 15$ ; 1988–1991). The *stippled squares* are the islands which had juveniles dispersing either from or to them during the study. The *arrows* connect the natal island of a juvenile to the island it dispersed to. The *black squares* are the islands which no marked juvenile dispersed from or to during the study



**Fig. 3** The distribution of band-sharing scores between mated pairs ( $n = 23$ ) and between potential mates in the population ( $n = 220$  comparisons). The mean and variance of the band-sharing scores between mated pairs did not differ from what would be expected if individuals were mating randomly within the population

Of the 23 females 20 mated with the closest available adult male (87%) and 18 of the 23 males mated with the closest available female (78%). Of the 23 pairings 22 were between individuals who were either residents of the same island or of nearest neighbor islands. The mean and variance of the band-sharing scores between mated pairs (0.512;  $s^2 = 0.0159$ ; range 0.314–0.844) did not differ from what would be expected under a random mating hypothesis ( $P = 0.025$ ; Fig. 3). Sixteen mated pairs (68%) had band-sharing scores below the lower 95% confidence limit for first-order relatives (0.553–0.722; Fig. 4).



**Fig. 4** The distribution of band-sharing scores between mated pairs ( $n = 23$ ) compared to the distribution of band-sharing scores between first-order relatives identified using parentage analysis ( $n = 82$  comparisons)

### Population structure

Of all possible pairwise comparisons 30% ( $n = 616$  comparisons) were made for the 1990 adult population and 24% ( $n = 205$  comparisons) for the 1991 population. Limited amounts of DNA per individual precluded making all pairwise comparisons within the population for each year. Approximately 90% of the within-island band-sharing comparisons were made in 1990 and 1991. The between-island band-sharing comparisons were conducted with a subset of individuals from every island included in the study. Comparisons were made between adult residents on neighboring islands, on islands separated by intermediate distances (~400–500 m) and on islands that were on opposite sides of the study area (~700–800 m; 1990 comparisons, Table 1). Mean band-sharing was higher than expected if individuals were assorted randomly among islands on 2 of 11 islands (islands with more than one adult resident) in 1990 (see Fig. 1; island 14,  $n = 2$ ,  $P = 0.009$ ; island 15,  $n = 3$ ,  $P = 0.047$ ). The nearest neighboring island was <100 m for both islands (70 and 93 m). High Peak was 210 and 326 m from islands 14 and 15, respectively. There was no correlation between inter-island distance and the degree of band-sharing similarity within islands.

Mean band-sharing among adults in three of nine nearest-neighbor groups also differed significantly from random in 1990. Two groups had average band-sharing scores that supported a higher rate of dispersal among islands within groups than among islands within the population as a whole (Fig. 1; islands 4–9,  $P = 0.007$ ; islands 2–3,  $P = 0.012$ ). Islands 4–9 were defined as a nearest-neighbor group because they formed a linear array along a ridge and no island was more than 40 m from its nearest neighbor. The remaining group (islands 11 and 16) had a lower than average band-sharing score among adults than expected by chance ( $P = 0.033$ ). There was no pattern evident between inter-island distance and propensity

**Table 1** The number of band-sharing comparisons made within ( $n = 318$ ) and between ( $n = 298$ ) islands in 1990. The between-island analysis included pairwise comparisons among all of the islands listed (unless noted)

Within Islands	Band-sharing comparisons	Between islands	Band-sharing comparisons
1	55	2, 3	4
3	6	4, 5, 6	15
4	3	7, 8, 9	3
5	6	4, 5, 6, 7, 8, 9	22
8, 9	3	2, 3, 12, 13, 14	57
11	6	14, 15, 16	2
12	10	11, 16	40
13	2	1, 15	44
14	1	16–2, 3, 4, 5, 6, 8, 11, 12 <sup>a</sup>	17
15	10	High Peak – 10, 11 <sup>a</sup>	16
16	45	High Peak – 2, 3, 4, 5, 6,	78
High Peak	171	8, 11, 12, 16 <sup>a</sup>	

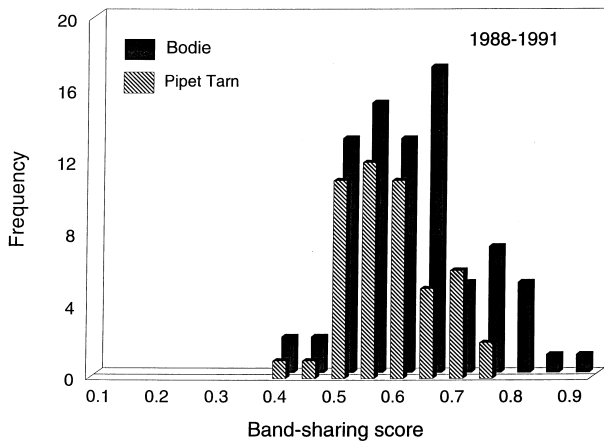
<sup>a</sup> Only individuals from island 16 and High Peak were compared to individuals from the other islands in the list

**Table 2** Band-sharing scores between adults on islands separated by >300 m did not differ significantly from random for five of the six groups examined (two-tailed randomization test)

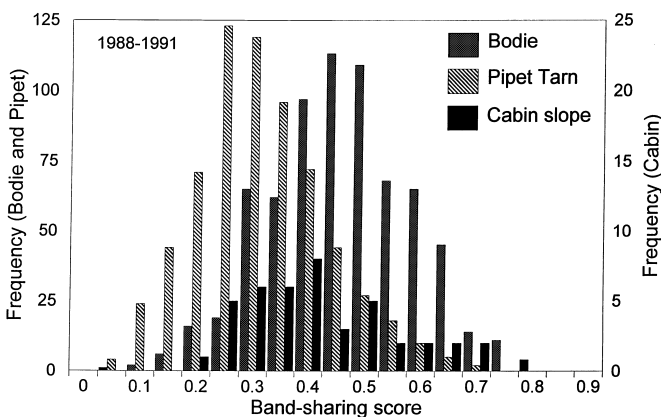
Islands	Distance between islands (m)	$P$ values
High Peak and 4–9	527	$P = 0.006$
High Peak and 2–3	380	$P = 0.396$ ns
11 and 2–3	835	$P = 0.222$ ns
11 and 4–9	754	$P = 0.177$ ns
16 and 2–3	698	$P = 0.052$ ns
16 and 4–9	492	$P = 0.285$ ns

to group. Islands separated by 15 m did not cluster while islands 200 m apart did (islands 2–3). The average distance between islands which did cluster was 111.8 m ( $SD \pm 64.66$ ), while the average distance between islands that did not cluster was 76.4 ( $SD \pm 55.33$ ). However, the two nearest-neighbor groups which clustered with high band-sharing were >300 m from High Peak suggesting an effect of distance from the mainland. Band-sharing data between adults on islands separated by >300 m, however, did not differ from random assortment for five of six groups examined (Table 2).

Three islands had higher average band-sharing among resident adults than would be expected by chance in 1991 (island 12,  $P = 0.0001$ ; island 13,  $P = 0.014$ ; island 14,  $P = 0.019$ ). Island 14 had higher average band-sharing among resident adults both in 1990 and 1991. All three of the islands were <100 m from their nearest neighbor. There was also no pattern in 1991 between mean band-sharing among adults and inter-island distance. Four of seven nearest-neighbor island groups clustered in 1991. Two groups displayed higher average band-sharing than would be expected by chance (islands 12 and 14, 70 m apart; islands 10 and 11, 70 m apart). Islands 11 and 16 showed the same low band-sharing pattern in 1990 and 1991. Islands 4–9, a group that had a



**Fig. 5** The distributions of band-sharing scores between first-order relatives from Bodie ( $n = 82$  comparisons; 95% confidence interval 0.533–0.722) and first-order relatives from Pipet Tarn ( $n = 44$  comparisons; 95% confidence interval 0.547–0.784)



**Fig. 6** The distribution of band-sharing scores between adult residents of Bodie ( $n = 697$  comparisons, mean = 0.483, range 0.075–0.844) compared to the distribution of band-sharing scores between adult residents of Pipet Tarn ( $n = 659$  comparisons, mean = 0.336, range 0.076–0.727) and Cabin slope ( $n = 42$  comparisons, mean = 0.437, range 0.238–0.737), populations found in continuous habitat

higher than average band-sharing score in 1990, had a lower average band-sharing score than would be expected if individuals were assorting randomly among islands in 1991 ( $P = 0.009$ ).

### Metapopulation dynamics

Average heterozygosities for Bodie ( $H = 0.736$ ) and Pipet Tarn ( $H = 0.709$ ) were virtually identical. The theoretical values for heterozygosity range from 0 (completely homozygous) to 1. Band-sharing distributions of first-order relatives, identified via DNA fingerprinting band-sharing analysis, also overlapped extensively between Pipet Tarn and Bodie (Fig. 5). Although the average band-sharing among first-order relatives (0.638) and average populationwide band-sharing (0.483) were higher at

Bodie than Pipet Tarn (0.603 and 0.336 respectively), this is not surprising given the isolated nature of this population. The distributions of band-sharing scores between residents of Bodie, Pipet Tarn, and Cabin slope were also very similar (Fig. 6). These data indicate that although Bodie is an isolated population with highly fragmented habitat, genetic variation comparable to non-isolated populations in nonfragmented habitat has been maintained.

## Discussion

### Dispersal

Juvenile dispersal patterns at Bodie were not different from patterns found in populations in continuous habitat (Smith and Ivins 1983; Peacock 1997). Juveniles tended to colonize the closest available territory whether on their natal island or on a nearest-neighboring island. Dispersal dynamics in both habitat types (fragment and non-fragmented) support a competition-for-resources hypothesis, where the predominant resource is a territory (Moore and Ali 1984; Dobson 1985; Peacock 1997). Territory occupancy is important to survival during the winter and only territorial individuals are known to reproduce in this species. Pika natural history and the dispersal patterns of marked juveniles are consistent with the assumptions of a competition-for-resources model by Waser (1985): (1) individuals do not share territories, (2) adults (residents of a territory) can displace younger individuals (nonresidents), (3) when forced to move, individuals settle on the first uncontested site they find, and (4) uncontested sites arise through the death of adults. However, enough movement takes place among islands that this spatial structure has resulted in only limited, transitory genetic subdivision within this population. The band-sharing distribution, among adults both within and between islands, suggests that the northern half of Bodie is panmictic.

### Mating

Juveniles tended to colonize the closest available home range and mated pairs tended to be neighbors. Despite this pattern there was no systematic inbreeding at Bodie. DNA fingerprinting data showed that band-sharing scores between mated pairs did not differ from a pattern of random mating. Even if a neighbor is chosen as a mate, multiple, short-distance dispersal targets for juveniles and occasional long-distance dispersal events have resulted in a low probability of mating with close kin. In contrast, DNA fingerprinting band-sharing scores between mated pairs in the Pipet Tarn population in continuous habitat suggest mate choice of individuals that are intermediately related (Peacock and Smith 1997).

Two possibilities could disrupt a pattern of moving to find a mate for underlying genetic reasons: (1) predation risk could preclude extensive movement between islands

for mating purposes; or (2) average band-sharing in the population is high enough that there is no genetic advantage in seeking out unrelated or intermediately related individuals. Two lines of evidence suggest that predation risk is the better explanation. First, average heterozygosity for Pipet Tarn and Bodie is virtually the same, which suggests Bodie is not highly inbred. The average heterozygosity estimates are comparable to estimates from species considered outbred (humans, lions, and domestic cats; Stephens et al. 1992). Second, the distributions of band-sharing scores between known first-order relatives for both populations are similar. Although average band-sharing within the population is higher at Bodie, the population-wide distributions of band-sharing scores showed considerable overlap between these two populations. These data suggest that higher average band-sharing at Bodie is the result of the relative isolation of this population (the nearest population is ~10 km away over non-talus habitat) and not an effect of habitat fragmentation *per se*.

The risks associated with moving between islands at Bodie to find mates may constrain individuals in mate choice, and thus promote mating between neighbors. Dispersal in fragmented habitat has resulted in a pattern of random mating in the pika despite constraints on mate choice. Random mating at Bodie appears to be an incidental effect of dispersal in fragmented habitat. Mate selection shaped by constraints on dispersal is evident from other species. Hoogland (1992) and Pugh and Tamarin (1988) found evidence of high levels of moderate inbreeding within home colonies of prairie dogs (*Cynomys ludovicianus*) and in a natural population of meadow voles (*Microtus pennsylvanicus*). However, these patterns did not differ from random mating in these populations. Individuals dispersing to different populations suffered high predation rates which favored a within-population dispersal pattern in both of these species. High levels of inbreeding in naked mole rat (*Heterocephalus glaber*) colonies are attributed to ecological constraints such as physical barriers to solitary dispersal (hard soils) and patchy food resources. These barriers apparently increase the fitness benefits of remaining in the natal colony relative to dispersing (Reeve et al. 1990). Distances between populations of rock (*Heterohyrax brucei*) and bush hyrax (*Procavia johnstoni*) on Serengeti kopjes limit dispersal and have resulted in inbreeding and genetic isolation (Hoeck 1989).

#### Metapopulation dynamics

The prominent difference in physical geography between the northern and southern halves of Bodie is the presence of High Peak in the north. The dispersal and population genetic data from this study, coupled with the extirpation of the southern islands, suggest that High Peak acts as a mainland in the northern half of the population. The additional component of juvenile dispersal to occupied islands also appears to be important to island occupancy

rates, island persistence, and maintenance of genetic variation. As a result, a stepping-stone model may explain gene flow at Bodie better than a basic mainland-island model (MacArthur and Wilson 1967; Gilpin 1990). Band-sharing among adults on High Peak, as well as on some of the peripheral islands of the study area (>500 m from High Peak) did not differ from what would be expected if individuals were assorted randomly among islands. These data suggest that gene flow is occurring throughout this population even though individuals typically disperse to nearest-neighbor islands. A stepping stone model by Gilpin (1980) predicts that if an island is half the distance between the source and target islands the stepping stone island will "capture" colonists and relay them to the target island. The islands in the north half of Bodie are configured more or less concentrically with the first tier of islands around High Peak roughly intermediate between High Peak and the second tier of islands. Individuals from High Peak that disperse to the first tier do not have to move on to the target islands themselves. Gene flow from High Peak would be accomplished if their offspring disperse to the next tier in the following generation.

Dispersal between islands at Bodie is in dynamic flux. Long-distance dispersal has been shown to be especially important in maintaining metapopulation integrity (Fahrig and Paloheimo 1988). Although no dispersal events were recorded during the study of individuals marked on High Peak to other islands in the population, genetic analysis suggests that individuals are moving from High Peak to the other islands and probably also from the islands to High Peak. Results of 20 years of census data (Smith and Gilpin 1997) show that subpopulations on islands at Bodie frequently go extinct and the islands are then recolonized. If juveniles disperse to the neighboring islands prior to extinction, the genetic variation from the original island is effectively conserved.

#### Conclusions

Single-species comparisons between populations found in habitat with different spatial structures allow us to identify the population parameters affected, as well as how they are affected, by habitat fragmentation. There are few examples of within-species variation in either dispersal patterns or mate selection that is due to habitat spatial structure. DNA fingerprinting data from this study suggest a within-species variation in the mate selection patterns of the pika that can be directly attributed to differences in the spatial structure of the habitat. More striking is the counterintuitive effect habitat fragmentation has had on mating patterns in the pika, i.e., random mating versus increased inbreeding. The extirpation of the population in the southern half of the study site, which did not have a mainland comparable to High Peak, provides evidence that mainland-island metapopulations are more resistant to extinction. The movements between smaller islands and from smaller islands to the mainland



are considered trivial to regional persistence of a mainland-island metapopulation. However, the results of this study suggest that these movements are an important contribution to island occupancy rates and the maintenance of genetic variation in this population.

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