Dispersal, Gene Flow, and Allelic Diversity between Local Populations of Thomomys bottae Pocket Gophers in the Coastal Ranges of California

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DISPERSAL, GENE FLOW, AND ALLELIC DIVERSITY BETWEEN LOCAL POPULATIONS OF *THOMOMYS BOTTAE* POCKET GOPHERS IN THE COASTAL RANGES OF CALIFORNIA

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Abstract.—We studied *Thomomys bottae* pocket gophers from 1979 to 1982 to determine if the amount of gene flow between local populations was sufficient to reduce allele frequency differences between them. Dispersal was quantified using three different trap techniques, and genetic changes in the population were monitored using protein variants. Additional allele frequency data were available for 1976 and 1977. We observed dispersal to be common in pre-reproductive juvenile females throughout the breeding season of their birth. Males on the other hand tended to disperse only from the end of the breeding season. Although dispersal was common, 63% of adults appeared to be recruited within 40 m of where they were born. Gene flow occurred into both established populations and into vacant habitat, but it was too low to reduce the differences in gene frequencies between the fields over seven years. We conclude that allelic diversity in *T. bottae* populations is a balance between random drift due to small effective population size and gene flow.

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The degree to which gene flow can reduce genetic differences between populations is unresolved (Ehrlich and Raven, 1969; Slatkin, 1985*a*, 1987; Caccone, 1985). In part, the debate continues because gene flow is difficult to quantify by direct measure in real populations, and little is known about dispersal patterns of most species (Jackson and Pounds, 1979). Other studies have attempted to measure gene flow indirectly using parameters such as Wright's (1965) F_{ST}, Slatkin's (1981) conditional allele frequency, $\bar{p}(i)$, or the distribution of private alleles (Slatkin, 1985*b*). Although these methods produce concordant estimates of gene flow in many insect species (Daly, in press), other studies yield contradictory estimates between the different genetic parameters (Larson et al., 1984; Caccone, 1985; Johnson et al., 1988) or between direct and indirect estimates of gene flow (Easteal and Floyd, 1986; Johnson et al., 1988).

Thomomys bottae pocket gophers have a high level of genetic differentiation within and between populations, in both karyotype and allozyme variation (Patton and Yang, 1977; Patton and Feder, 1981). The subterranean mode of life of pocket gophers is associated with low vagility, philopatry, and small effective population size, N_e (Howard and Childs, 1959; Vaughn, 1963; Williams and Baker, 1976; Nevo et al., 1974; Nevo, 1979; Patton and Feder, 1981; Williams and Cameron, 1984). Yet despite these characteristics, several genetic studies of *T. bottae* conclude that moderate gene flow between populations must occur, and is important in determining both morphological differences and allelic diversity within and between populations and in the maintenance of the high levels of individual heterozygosity (Patton and Yang, 1977; Patton and Feder, 1981; Slatkin, 1981; Smith and Patton, 1984); and is one of the factors that determines the degree of introgression between chromosomal races in their contact zones (Hafner et al., 1983).

We studied dispersal and gene flow in *T. bottae* to determine if the amount of gene flow (= genetic exchange) that was occurring between local populations was sufficient to reduce allele frequency differences between them. Data were available spanning seven years, which is about seven generations (Howard and Childs, 1959). We used a variety of direct and indirect measures of gene flow to gain a consistent view of the phenomenon. This is the first such study of *T. bottae*.

Patton and Feder (1981) reported on the genetic consequences of extinction and recolonization in the same populations. They observed that the effective population size,

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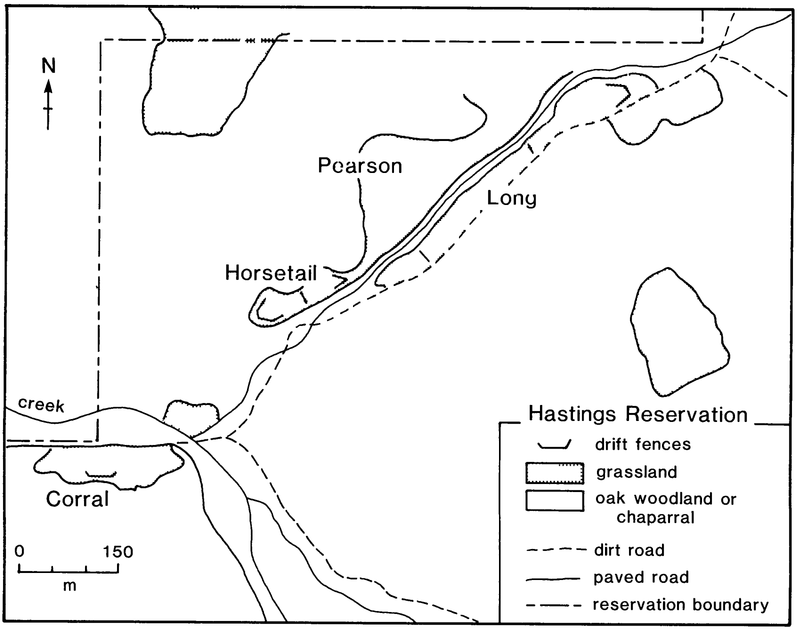

FIG. 1. Map of Hastings Reservation, Carmel Valley, Monterey Co., California. The three study fields and the position of the drift fences are indicated.

N_e, was small: adults were grouped into small demes in which females were more frequent than males (inbreeding N_e) and male reproductive success was highly variable (variance N_e). Gene frequency differences between the populations was high, and there was a significant deficiency of heterozygotes, both of which are expected consequences of small N_e. Twelve months later the fields had been recolonized by gophers that were younger than the original residents. Gene flow had reduced allele frequency differences between the fields. Patton and Feder (1981) proposed that a subsequent period of stability in the population would again increase allele frequency differences between the fields.

This study reports on the same populations two to five years later. Observations were made almost continuously for eight months of the year to determine the time of year that dispersal occurred, the sex, age and reproductive condition of dispersers, and the genetic consequences of this dispersal. Pocket gophers are suitable particularly for this kind of study. Adults of both sexes live in solitary, discrete territories, which can be detected on the surface during the breeding season by fresh earthen mounds that the animals produce as they excavate tunnels or by a fresh plug of earth that is produced as the gopher feeds (Howard and Childs, 1959). Thus, during the breeding season, it is possible to remove all adults from a field and then detect any subsequent immigrants into the field. Further, it makes it possible to mark most, if not all, adults in the population (Howard and Childs, 1959).

MATERIALS AND METHODS

Fields.—We observed pocket gophers in three of the grassland fields (Horsetail, Long, and Corral fields) at the Hastings Natural History Reservation, Carmel Valley, Monterey Co., California, between 1979–1983. Additional data were available for 1976–1977 from an earlier study (Patton and Feder, 1981). The reservation represents typical gopher habitat in the coastal ranges of California (unpubl. data). Although our estimates of dispersal were limited by the extent of trapping, the fields were separated by areas of oak woodland, chaparral, and riparian vegetation (Fig. 1), habitats not favored by the gophers. Nearby grasslands were also searched and trapped to detect marked dispersers. Records of such individuals are included in the analysis below. Thus, we were able to detect dispersal within 300–400 m of the initial site of capture.

Animals were sampled with replacement in two control fields (Horsetail and Long) while the gophers were actively tunneling (November–June) using either live-traps placed in the gophers' subterranean tunnels (Howard and Childs, 1959) or in pitfall traps placed across the middle and at either end of these two control fields (Fig. 1). Part of each field was sampled for four to five consecutive days every four to six weeks. Traps were placed so that an individual could be caught a number of times in its territory, and all areas of activity in the two fields were sampled in an attempt to enumerate the population. Animals were tagged and a blood sample taken by cardiac puncture for genetic analysis. To obtain estimates of longevity we assumed that any untagged adult caught in 1981 or 1982 had been born the previous spring because dispersal in adults was very uncommon (see below) and most adults in the field could be trapped (Howard and Childs, 1959). Details of the trapping techniques are given elsewhere (Daly and Patton, 1986).

The population in the experimental field (Corral field), which was isolated from the two control fields (Fig. 1), was live-trapped in winter and spring 1980. In winter 1980/81 and 81/82 the resident population was removed using kill-trapping techniques described by Patton and Feder (1981). Subsequent immigrants were removed during the following spring. Tissue samples and skulls were preserved.

Live-trapping and kill-trapping ceased during May each year because of poor trap response when the soil started to dry out. Pitfall trapping, however, continued to catch gophers until July when the trapping ceased.

Electrophoresis.—Tissues were examined by starch gel electrophoresis (Patton et al., 1972; Patton and Feder, 1981) for the variable enzyme systems, isocitrate dehydrogenase (ICD-1), 6-phosphogluconic dehydrogenase (PGD), peptidase (PEP-1) and transferrin (TRF). We examined a fifth enzyme, adenosine deaminase (ADA) on cellulose acetate gels (Cellogel, Chemetron, Italy) with a 20 *mM* Tris 5 *mM* EDTA maleic acid buffer, pH 7.8 (150 volts, 40 minutes). The alleles of each locus were numbered (1 to 4) corresponding to the relative mobility of the equivalent allozyme, starting from the anode.

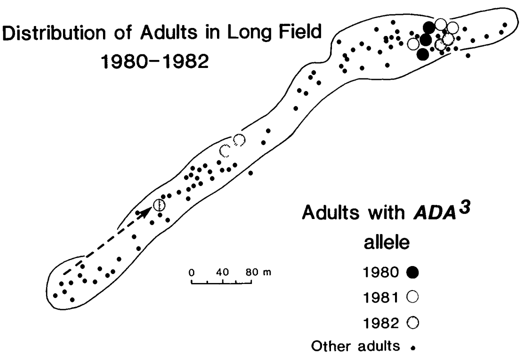

FIG. 2. Distribution of all adults in a control field (Long field) in 1980–1982. Those carrying the *Ada*-^{3} allele are indicated by large circles. One such adult dispersed from its initial place of capture as a juvenile, indicated by the arrow.

Statistical Analyses.—Gene frequencies in the population were examined with G-tests using the computer program GLIM 3.77 (Payne, 1985). Comparisons between adults and juveniles were made for animals caught only in the same year in the same field. The gene frequencies observed by Patton and Feder (1981) were included in the analysis. The variance in allele frequencies between samples from the three fields were computed using Wright's *F*-statistics as described by Patton and Feder (1981). Data from 1976–1977 were recalculated using only the five loci sampled from blood tissue.

RESULTS

Direct Observations of Movements

Adult Populations in Control Fields 1980–1982.—The adult populations in the two control fields were characterized by a female-biased sex ratio and a high annual turnover of both sexes; those adults that did survive were extremely sedentary but of the few that did move, most were male.

Reproduction started in response to rainfall in autumn and winter and ceased as the vegetation dried out in spring so the duration of the breeding season varied from year to year. In 1979/80 and 1981/82 breeding

TABLE 1. Size (*N*) and sex ratio of adult populations of *Thomomys bottae* in 1976–1977 (from Patton and Feder, 1981) and in 1980–1982. In 1981–1982, the population in the experimental field was those animals removed by kill-trapping in autumn prior to the breeding season. All other animals were live-trapped during the breeding season.

	Ratio females/males (*N*)			
		Control fields		
Year	Experimental field	(HTF)	(LF)	Total
1976	2.9 (27)	1.4 (12)	2.6 (29)	2.3 (68)
1977	4.0 (40)	3.6 (23)	1.8 (25)	3.0 (88)
1980	2.2 (19)	3.5 (77)	1.9 (84)	2.5 (180)
1981	2.5 (56)	2.5 (77)	1.6 (121)	2.0 (254)
1982	2.4 (20)	2.4 (44)	2.2 (80)	2.3 (144)

commenced in December but was delayed in 1980/81 until late February. Breeding ceased in May in all years.

Population turnover was high, but females lived longer than males: in 1981, only 17% of males and 29% of females were greater than one year old; and in 1982, 26% and 44%, respectively (see Table 1 for sample sizes). In 1982, only 8% of males and 13% of females were at least three years old. These results are consistent with estimates of longevity obtained only from tagged animals. Of all adult males tagged in one year, only 19% (22/115) survived to the following year compared with 31% of females ($\chi^2 = 5.6$, $df = 1$, $P < 0.05$, for differences in survival between sexes).

The adult sex ratio was skewed significantly towards females in three years 1980–1982 ($\chi^2 = 65$, $df = 1$, $P < 0.001$) which arose partly because adult females lived longer than males: the sex ratio was 1.7:1 (sample size, $N = 77$) for one year olds compared with 3.7:1 ($N = 46$) in older animals.

The number of adults in the two control fields in 1980–1982 varied between 124 and 198 (Table 1). The decline in the adult population between 1981 and 1982 was not a result of poor adult survival as 50 adults greater than one year old in 1981 compared with 47 in 1982. Rather, it resulted from reduced recruitment of one year olds, 148 in 1981 compared with 77 in 1982, which may have been a result of the shorter breeding season in 1981.

Dispersal by adult gophers could be followed using either pitfall traps or live-traps. We defined adult dispersal as any movement in which the gopher changed its territory. Thus, an adult was assumed to have moved if it was trapped on two or more occasions at least 40 m from any of its other trap captures. This distance was chosen as it represented the minimum distance between non-adjacent territories (Daly and Patton, unpubl.).

A total of 400 different adults were trapped, yet the live-traps detected only five males and two females to change territories. Six individuals moved between 40–100 m and the other one moved 300 m. Both females were nulliparous when trapped in the first location but were observed to reproduce in their new territory. Two of the five males were sexually mature (scrotal testes) in their new territory. One had also been sexually mature as a one year old. All other adults in the population that survived for two or more years as adults occupied the same territory in successive years with only minor adjustments in boundaries.

Pitfall traps caught 16 adult males and 3 adult females of which 9 males and 1 female were caught in autumn or winter before the breeding season. All these individuals must have been trapped while on the surface but they may not have been dispersing. Indeed, two males and one female were resident in territories transversed by the pitfall line at the time of their capture. However, some animals were dispersers; two males were caught >100 m, and 1 male >250 m, from their last sites of capture.

Adult Populations in the Experimental Field 1980–1982.—Population size varied between 19–56 and the sex ratio was skewed to females in all three years (Table 1; $F_{[1,2]} = 150$, $P < 0.001$) and did not differ from that in the control fields. Dispersal of adults or sub-adults occurred in two time periods:

TABLE 2. Mean body weight (standard deviation = SD), and proportion molting and breeding, in juvenile *Thomomys bottae* pocket gophers that were caught in spring 1981 and 1982 in the control fields either underground using live-traps or above ground in pitfall traps; or were dispersing into the experimental field.

	Control				Experimental	
	Underground		Above ground		Dispersing	
	M	F	M	F	M	F
(1) 1981						
Mean body weight (g)	60	51	52	41	68	47
SD	18	11	15	18	27	14
N	12	6	31	38	4	15
Proportion molting	0.23	0	0.25	0.15	0	0.13
Proportion breeding	0	0.17	0	0	0	0
(2) 1982						
Mean body weight (g)	84	81	73	58	88	68
SD	31	20	25	16	26	16
N	62	87	58	71	13	21
Proportion molting	0.50	0.69	0.44	0.23	0.66	0.24
Proportion breeding	0	0.48	0	0.09	0	0.05

during summer to early autumn and also during spring.

The majority of summer/autumn dispersal was of nulliparous females born the previous spring. The 13 females and 7 males present in winter 1981/82 must have dispersed into the field during the previous summer and autumn because no gophers were present when trapping ceased in June 1982. Pocket gophers can be aged by a cranial suture closure score, which is correlated with chronological age (Daly and Patton, 1986). Using this method we determined that only one male and one female disperser were more than two years old compared with 10 females and 5 males which were one year old or less (two females and one male could not be classified). Also, 11 of the 13 females were nulliparous.

Adult dispersal also occurred in spring. In general, these adults were sexually active and there was not a strong sex-bias. Twenty-four percent (17/70) of all dispersers into the field in spring were adults: four males and females in 1981 and four males and five females in 1982. Seven of the nine females were either pregnant or lactating while six of the eight males had testes greater in length than 16 mm which indicated that they were capable of producing viable sperm (Gunther, 1956).

Population Parameters of Juveniles and Sub-adults.—Gophers dispersing into the experimental field and caught above ground in the control fields tended to be young, pre-reproductive individuals, and were more likely to be female; dispersal began as soon as juveniles were present on the reservation (late winter) and continued into summer although males tended to delay dispersal until late spring.

Juveniles appeared simultaneously in all three types of trap, six to eight weeks after mated females were first observed. All juveniles trapped in the experimental field (kill-traps) had dispersed because this field was kept free of adults throughout spring. However, in the control fields it usually was not possible to distinguish between juveniles caught in their natal territory from those that had dispersed, although juveniles caught in pitfall traps must have been above ground. Above ground movement appeared common and pitfall traps accounted for 80% of juveniles trapped in 1981 and 48% in 1982.

Table 2 summarizes the characteristics of juveniles at their time of first capture in 1981 and 1982. The two years differed; fewer juveniles were caught during the shorter breeding season of 1981 ($N = 106$ cf. 312), and at first capture they were lighter ($F_{[1, 417]} = 104, P < 0.01$), pre-reproductive and very few were molting, compared with 1982 (Table 2). Females outnumbered males in 1982 (1.3:1, $\chi^2 = 5.6$, $df = 1$, $P < 0.025$) and the bias was present even in very young gophers, those less than 40 g in body weight (1.82:1, $N = 62$).

In 1981, dispersal into the experimental field was strongly female biased, particularly compared with the ratio observed in the control fields ($\chi^2 = 5.4$, $df = 1$, $P < 0.05$). This bias was less evident in 1982 ($\chi^2 = 0.3$, $df = 1$, $P > 0.05$). No strong bias in sex ratio was observed in the animals caught in the control fields, although more females were caught than males (Table 2).

Females moving above ground were generally young and pre-reproductive. Those caught in pitfall traps in the control fields appeared to be the youngest: they were significantly lighter than females either live-trapped in the control fields ($F_{[1,\,334]} = 43$, $P < 0.01$) or dispersing into the experimental field ($F_{[1,\,200]} = 54$, $P < 0.01$). Females dispersing into the experimental field were intermediate in weight but were still significantly lighter than females in live-traps in both 1981 ($F_{[1,\,17]} = 4.6$ $P < 0.05$) and in 1982 ($F_{[1,\,32]} = 133$, $P < 0.05$).

Females moving above ground were less likely to be parous (pitfall: $\chi^2 = 35$, $df = 1$, $P < 0.001$; kill: $\chi^2 = 17$, $df = 1$, $P < 0.001$) and to have commenced to molt into their adult pelage (pitfall: $\chi^2 = 33$, $df = 1$, $P < 0.001$; kill: $\chi^2 = 14$, $df = 1$, $P < 0.001$) than were juvenile females live-trapped in these fields. Furthermore, most of the females that were molting had just begun to do so (14/16 in pitfall traps; 4/5 in kill-traps). Dispersal may be associated with the commencement of these events as 24% (5/21) of the nulliparous females dispersing into the experimental field were showing signs of first estrus.

In contrast, there were no apparent differences between juvenile males in control or experimental fields: they were approximately the same body weight ($F_{[3,\,75]} = 0.07$, $P > 0.05$) and the proportion which were molting when at first capture was similar ($\chi^2 = 2.5$, $df = 2$, $P > 0.05$). Sexual maturity was not observed in any of the juvenile or subadult males.

The pattern of above ground movements in both experimental and control fields was not the same in males and females. Young females moved throughout the spring while males seemed to delay their movements until late spring when they were heavier and the surface soil and the grass started to dry out. In April 1982, when captures of juveniles had become common, males in the control fields were difficult to trap above or below the ground and few males (3 in 13) dispersed into the experimental field; the sex ratio of all new captures was 3.3:1 ($N = 90$). However, more males were caught in May (0.62:1, $N = 110$) in all the three kinds of traps. Overall, females were significantly lighter at first capture than were males ($F_{[1,282]} = 9.8$, $P < 0.001$) and those caught dispersing or moving above the ground were also less likely to be molting into adult pelage than were males (Table 2).

Dispersal by Juveniles and Sub-adults in the Control Fields.—Trapping results in the control fields indicate a moderate degree of philopatry in the populations. Sixty individuals were caught as juveniles on at least two occasions more than two weeks apart; 73% (24 males, 20 females) were last seen within 40 m of their original place of capture, 18% (7 males, 4 females) had moved between 40–100 m, and 8% (4 males, 1 female) moved between 100–200 m.

Forty-six individuals were caught both as a juvenile and an adult; 63% (5 males, 24 females) were recruited into the adult population within 40 m of their first site of capture when a juvenile, 20% (3 males, 6 females) between 40–100 m, 11% (5 females) between 100–200 m and the last 6% (2 males and 1 female) had moved between 200–300 m. Movement was in all directions within each field and two individuals moved between the two control fields. These results are consistent with those obtained by genetic analysis of the population (see below).

Genetic Structure of the Population

Allele Frequencies.—Allele frequencies for five polymorphic loci in adults in both the control and experimental fields from 1976–1982 are given in Table 3. *G*-tests indicate that frequencies within fields were consistent over time and that differences between the fields were maintained over the seven years.

Within each field, allele frequencies did not change significantly over the seven years between 1976 and 1982 (Table 4, 'Year' term). The *G*-tests may lack power to detect some year-to-year variation, particularly in the experimental field. For example, large changes in allele frequency were observed in this field for *Trf* and *Pgd* (Table 3). How-

TABLE 3. Summary of allele frequencies for five polymorphic loci of adult *Thomomys bottae* in control and experimental fields. Data for 1976 and 1977 are derived from Patton and Feder (1981). Sample sizes are given in Table 1.

Allele		Control (HTF)				Control (LF)				Experimental			
Locus	Year	1	2	3	4	1	2	3	4	1	2	3	4
Icd	1976	0.17	0.46	0.38	–	0.27	0.39	0.34	–	0.08	0.46	0.46	–
	1977	0.23	0.50	0.27	–	0.11	0.50	0.39	–	0.15	0.54	0.31	–
	1980	0.25	0.40	0.34	–	0.08	0.43	0.49	–	0.21	0.43	0.36	–
	1981	0.19	0.44	0.37	–	0.09	0.42	0.50	–	0.21	0.35	0.45	–
	1982	0.12	0.49	0.38	–	0.11	0.53	0.36	–	0.13	0.38	0.5	–
Pep-1	1976	1.0	0	–	–	0.94	0.06	–	–	0.94	0.06	–	–
	1977	0.98	0.02	–	–	0.95	0.05	–	–	1.0	0	–	–
	1980	0.99	0.01	–	–	0.95	0.05	–	–	1.0	0	–	–
	1981	0.99	0.01	–	–	0.98	0.02	–	–	0.98	0.02	–	–
	1982	1.0	0	–	–	0.94	0.06	–	–	0.96	0.04	–	–
Trf	1976	0.77	0.23	–	–	0.63	0.38	–	–	0.37	0.63	–	–
	1977	0.80	0.20	–	–	0.56	0.44	–	–	0.52	0.48	–	–
	1980	0.68	0.32	–	–	0.53	0.47	–	–	0.46	0.54	–	–
	1981	0.70	0.30	–	–	0.48	0.52	–	–	0.54	0.46	–	–
	1982	0.69	0.31	–	–	0.58	0.42	–	–	0.65	0.35	–	–
Pgd	1976	0.75	0.25	–	–	0.92	0.08		–	0.93	0.07	–	–
	1977	0.88	0.13	–	–	0.96	0.04	–	–	0.96	0.04	–	–
	1980	0.90	0.11	–	–	0.97	0.03	–	–	0.93	0.07	–	–
	1981	0.87	0.13	–	–	0.97	0.03	–	–	0.83	0.17	–	–
	1982	0.84	0.16	–	–	0.95	0.05	–	–	0.91	0.09	–	–
Ada	1976	0.04	0.88	0.04	0.04	0.02	0.92	0.02	0.05	0	0.89	0.09	0.02
	1977	0.13	0.80	0.02	0.05	0.05	0.90	0	0.05	0.02	0.94	0.02	0.02
	1980	0.08	0.84	0.01	0.06	0.03	0.88	0.02	0.07	0.04	0.94	0	0.02
	1981	0.05	0.86	0.01	0.08	0.03	0.87	0.04	0.07	0.01	0.95	0.03	0.01
	1982	0.04	0.84	0.03	0.08	0.06	0.84	0.04	0.06	0	1.0	0	0

ever, there were significant differences in allele frequencies maintained between the two control fields for four of the five loci ('Field' term in Table 4) and between the control and experimental fields (all $P < 0.001$). Both common and low frequency alleles contributed to the variation between the fields (Table 3).

Significant differences between allele frequencies in adults and juveniles within each field were also observed in both control and experimental fields ('Age' term, Table 4). This is not unexpected given the large differences in reproductive success observed between adult males (Patton and Feder, 1981).

F-Statistics.—The values of the F-statistics indicate that there was significant population differentiation despite estimates of immigration of 8 –18 individuals per generation.

Wright's (1965) F-statistics are a measure of population differentiation. F_{ST} measures the degree to which this differentiation occurs between sub-populations. The values given in Table 5 are consistent with the analysis of allele frequencies above; differences between the fields were maintained over 1976–1982 although the values of F_{ST} were not statistically different in all years. The statistical significance of the values in 1980 and 1981 reflect the larger sample sizes available for those two years. The data quoted for 1976–1977 differ from those in Patton and Feder (1981) who estimated F-statistics for four fields using 11 variable protein loci.

F_{ST} can estimate the rate of gene flow from the relationship $F_{ST} = 1/(1 + 4Nm)$ for neutral alleles in the infinite island model of population structure (Wright, 1931). Nm gives an estimate of the number of migrants per generation into each sub-population. The values of Nm from the five loci are between 8 to 18 (Table 5).

F_{IS} is a measure of the deviation from random mating within a field. Mating within our population was not random. Over

TABLE 4. χ^2 values (and degrees of freedom) for G-tests, which examined variation in allele frequencies in the control and experimental fields (i) in adults among the five years ('Year' term), (ii) in adults among the two control fields ('Field'), (iii) among adults and juveniles ('Age').

	Control fields			Experimental field	
Locus	Year	Field	Age	Year	Age
Ada	11.1 (12) ns	4.9 (3) ns	9.8 (3)*	15.1 (12) ns	7.6 (3) ns
Pgd	7.0 (4) ns	30.1 (1)***	35.4 (1)***	8.6 (4) ns	0.2 (1) ns
Pep	3.3 (4) ns	15.0 (1)***	31.8 (1)***	5.9 (4) ns	5.9 (1)*
Icd	18.3 (8)*	17.6 (2)***	5.3 (2) ns	12.1 (8) ns	7.0 (2)*
Trf	7.3 (4) ns	32.8 (1)***	0.2 (1) ns	9.3 (4) ns	1.2 (1) ns

ns, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

the study period, values of F_{IS} became increasingly more positive; that is, there was an increasing deficit of heterozygotes. These results are consistent with the Wahlund effect from subdivision of populations.

Distribution of Alleles at Low Frequency.—The distribution of low frequency alleles from year-to-year indicates a moderate degree of philopatry within the populations in the control fields.

Four alleles were found at frequencies less than 0.05 throughout the study area: *Ada-*^{3}, *Ada-*^{4}, *Pgd-*^{2} and *Pep-1*^{2}. As the population size of each field was between 60 and 100 individuals, fewer than 6 individuals carried these alleles. Because of the high annual turnover of adults (see above), most adults with a genotype containing one of these alleles were unlikely to be present in the population for more than one breeding season. Thus, the degree of philopatry can be estimated from the distribution of these alleles from year-to-year.

The distribution in one of the control fields (LF) of adults carrying the *Ada-*^{3} allele in the years 1980–1982 is illustrated in Figure 2. Only three male adults carried this allele in 1980 and they were all located in one part of the field less than 25 m from each other. None of these three survived to 1981 but again three adults (two females and one male) carrying this allele were observed within the same small area. Two new adults were observed in 1982. The allele was also observed in the middle of the field in 1981 and 1982. Two females occupied adjacent territories in both years midway down the field. A third female had been trapped as a juvenile at one end of the field and then dispersed before breeding as an adult (indicated by an arrow in Fig. 2). These data suggest that individuals often were recruited into a field close to where they were born. Nevertheless, gene flow occurred because these alleles appeared in parts of the field in which they had been absent.

We quantified these observations for both control fields by measuring the distance between the territory of an adult (either male or female) present in one year and the nearest territory in which an adult (either male or female) carried the same allele in the previous year. No adult was observed to occupy the same territory as any adult present the year before with the same low frequency genotype. The mean distance for all combinations was less than 60 m and 54% (28/52) of adults appeared to be recruited within 40 m of an adult of similar rare genotype. There did not appear to be any difference between males and females ($F_{[1, 3]} = 0.03$, $P > 0.05$).

A further measure of philopatry in the control populations can be derived from deviations in Hardy-Weinberg frequencies of the genotypes. For *Ada,* the less frequent homozygotes occurred much more frequently than expected ($\chi^2 = 269$, $df = 8$, $P < 0.001$). In particular, five individuals were

TABLE 5. F-statistics (F_{IS}, F_{ST}), tests of significance for F_{ST}, and estimates of the number of immigrants per generation (Nm), for adult populations from three fields, based on five loci. Levels of significance are given in Table 4.

Year	F_{IS}	F_{ST}	Nm
1982	0.128	0.014 ns	18
1981	0.071	0.023**	11
1980	0.054	0.024*	10
1977	0.008	0.030 ns	8
1976	−0.170	0.020 ns	12

observed with genotype *Ada*-^{33} when only 0.8 were expected in a randomly mating population. Thus, it appeared that some breeding did occur in the control fields between individuals that were likely to be related.

DISCUSSION

Our study demonstrates the importance of studying dispersal and gene flow using a number of complementary techniques: direct measures were made using three different trap techniques, and gene flow was estimated from the distribution of alleles, and from the genetic structure of the population. Each technique by itself would not have revealed the complex pattern of interactions between the demic structure of gopher populations, dispersal of juveniles and adults, and the recruitment of these dispersers into stable (control fields) populations and into habitat in which extinctions of populations had occurred.

We observed that dispersal in pocket gophers was common, yet in the control fields 63% of adults were recruited within 40 m of their presumed natal territory, and only two individuals dispersed between the two control fields. Gene flow occurred through the recruitment of immigrants into both established populations and vacant habitat. However, the amount of gene flow recorded did not reduce the genetic differences between populations in adjacent fields over a seven-year period.

Dispersal.—All three techniques used gave a consistent view of dispersal similar to those reported previously in *T. bottae* (Howard and Childs, 1959), *Pappogeomys castanops* (Smolen et al., 1980) and *Geomys attwateri* pocket gophers (Williams and Cameron, 1984). Most movement occurred in the gophers in spring and summer before they reached reproductive condition. Adult dispersal was not common although some reproductive adults did disperse during the breeding season. There were differences in the dispersal patterns of male and female *T. bottae* of all ages. Although more juvenile female *T. bottae* were observed to disperse, it is not clear if this was because females were more common in our population (see Williams and Cameron, 1984).

TABLE 6. A comparison of estimates of the number of immigrants per generation (*Nm*) between local populations of *Thomomys bottae* pocket gophers on Hastings Reservation and between populations sampled from the species range (Patton and Yang, 1977). Methods are Wright's (1965) F_{ST}, Slatkin's (1981) conditional allele frequencies, $\bar{p}(i)$, Slatkin's (1985*b*) private polymorphism, $\bar{p}(1)$, and from trapping records in control and experimental fields.

Method	Estimates of *Nm* between populations	
	Local	Species range
1. F_{ST}	8–18[1]	0.37–0.63[2]
2. $\bar{p}(i)$	≥2.5[3]	0.25[3]
3. $\bar{p}(1)$	n.a.[4]	0.86[2]
4. Observed[1]—Control fields	1–6[1]	n.a.
5. Observed[1,3]—Experimental fields	20–40	n.a.

[1] From this study; [2] from Patton and Yang (1977); [3] from Patton and Feder (1981); [4] n.a. = not available.

The results of the pitfall trapping clearly demonstrate that much of the dispersal occurred above ground. Adaptation to a subterranean way of life in *T. bottae* was not, in itself, sufficient to limit vagility as proposed by Nevo (1979). Although above ground movements have previously been reported in juvenile *T. bottae* during spring (Bryant, 1913; Imler, 1945; Howard and Childs, 1959), this study is the first to quantify its characteristics.

In spring, juvenile females started to disperse soon after they were weaned, which is when they began to molt into adult pelage and, in favorable years, when they can come into estrus. Dispersal at this time would reduce the chance of a consanguinous mating and, because gophers occupy solitary territories, a pregnant female would need to establish her own territory. In contrast, none of the males reached sexual maturity in the spring in which they were born. Dispersal was more likely to be delayed until late spring when dispersing males were heavier and more likely to be molting than were females. The greater size of sub-adult males at this time may help them compete for a territory with adult males (Williams and Cameron, 1984).

Gene Flow.—Dispersal was sufficiently common for vacant habitats (such as the experimental field) to be rapidly recolonized. The number of adult immigrants into the experimental field was 40 in 1977 (Patton and Feder, 1981) and 20 in 1982 (Table 6). Because of its geographic location relative to potential source populations, such movement must have been at least over several hundred meters.

Dispersal also gave rise to gene flow in established populations. Animals carrying alleles that were at low frequency in the population immigrated into parts of the control fields where that allele had been absent. Estimates of immigration into unperturbed fields can be made from trapping records (Table 6). The lower estimate of one individual per generation was the observed number of adult recruits that dispersed between the two control fields averaged over two generations (= years); clearly immigration would have exceeded this value as other source populations were present on the reservation. The upper estimate of six individuals was obtained from the proportion of adult recruits that had dispersed more than 200 m, which represents the minimum distance between suitable habitats.

Ephemeral populations in suboptimal habitats may also contribute to gene flow. In our study, we observed reproductive females at low density in small pockets of grassland removed from the main centers of activity, although occupation of these habitats was not continuous throughout the study. The importance of these ephemeral populations needs further investigation.

Although more females appeared to disperse in our populations, male immigrants had the potential to contribute significantly to gene flow. Patton and Feder (1981) used paternity analysis to demonstrate that there was a high variance in reproductive success among males, although females outnumbered males 2.5–3.5 to 1. In one case, five females had been inseminated by the same male. A successful male immigrant may therefore contribute as much to the gene pool in the next generation as 3–15 females. As a result, significant allelic differences could be expected between adults and juveniles, which was the case in our populations.

Genetic data can also give indirect estimates of the amount of gene flow, *Nm* (the number of immigrants per generation), that is occurring in *T. bottae.* In Table 6 we compare the results for the populations in our study area using a number of methods. Estimates are also available for 23 populations of *T. bottae,* sampled throughout the species range (Patton and Yang, 1977). All three indirect techniques give a consistent view of gene flow for *T. bottae*; moderate over the species range, and higher between adjacent populations. The realized amount of gene flow between our control fields, one to six individuals per generation, was less than that predicted from genetic methods, 8 to 18 individuals. However, estimates of potential gene flow from the experimental field, 20 to 40 adults in one generation, were a little higher than the predicted gene flow. These results support Slatkin's (1985*a,* 1987) hypothesis that in many species gene flow is variable and unpredictable and may occur more from recolonization after local extinctions than from a regular pattern of dispersal between established populations.

Wright (1931) showed that if $Nm > 1$, gene flow was sufficient to overcome local differentiation between populations when they are at equilibrium (see also Speith, 1974). This would seem to be contrary to our observations in *T. bottae* because consistent differences were observed between the populations for over seven generations despite gene flow. However, this relationship was developed for the infinite island model of population structure (Wright, 1931) in which a subpopulation receives immigrants at the rate of m individuals per generation chosen at random from other subpopulations, and it should be considered only a 'rule of thumb' when applied to finite populations (Speith, 1974). Wright (1969 pp. 292–293) indicated that small vales of F_{ST} can be associated with considerable genetic differentiation between populations if N_e is much less than the observed population size and if most immigrants come from neighboring demes (stepping stone model of gene flow, see also Slatkin, 1985*a* for further discussion). Both conditions are likely to be met in the Hastings populations (Patton and Feder, 1981; and this study).

More recently, Allendorf and Phelps (1981) have argued that the more correct interpretation of $Nm > 1$ is that populations will share the same alleles over long periods of evolutionary time; it does not necessarily mean that populations will have identical allele frequencies. Using simulation models, they demonstrated that significant allelic divergence between subpopulations still occurred in 50% of generations even when there was considerable gene flow ($Nm = 50$) and divergence occurred in most generations when $Nm = 10$.

These predictions (Wright, 1969; Allendorf and Phelps, 1981) are supported by our results with *T. bottae* populations from Hastings Reservation. Allelic divergence was maintained between populations despite moderate gene flow. However, populations shared all alleles and individual heterozygosities were high (Patton and Feder, 1981). We can use these results to understand the patterns of allelic diversity between populations of *T. bottae* throughout the species range (Patton and Yang, 1977). The demic structure of pocket gophers with more adult females than males, coupled with a high variance in male reproductive success, will result in low effective population size within local populations and large genetic differentiation between populations in all habitats. However, if gene flow can occur between populations, such as those in coastal California (Patton and Yang, 1977), high levels of individual heterozygosity can still be maintained. This is in contrast with isolated populations in desert or montane areas, which have very little potential for gene flow. As predicted from our results, these populations also have high genetic differentiation but it is coupled with low levels of individual heterozygosity (Patton and Yang, 1977).

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