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THE RELATION BETWEEN SPECIES NUMBERS AND ISLAND CHARACTERISTICS FOR HABITAT ISLANDS IN A VOLCANIC LANDSCAPE

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ABSTRACT.— Within the Craters of the Moon Lava Flow in southeastern Idaho are kipukas, islands of sagebrush habitat isolated by relatively barren lava. In 1979 I counted the number of species of plants, small mammals, and reptiles for a series of kipukas. The degree of isolation of a kipuka was not related to numbers of species found there; thus, these data do not support the equilibrium theory of island biogeography. For most of the study organisms lava is not a significant barrier to dispersal. Larger kipukas support larger numbers of species. For plants this relationship likely is a result of the increased topographic variety of larger kipukas, whereas for small mammal species minimum area requirements for maintaining populations are met only by larger kipukas. More distant kipukas showed increased density of small mammals, possibly as a result of reduced predation. Patterns of distribution in this ecosystem are best explained, not by any all-inclusive community mechanism, but through the agglomerative contributions of a variety of population and community functions.

The Snake River Plain in Idaho is a formation built up, over millions of years, of wind-blown loess deposits alternating with layers of volcanic materials from localized eruptions (Greeley and King 1975). The present manifestation of this geologic history is a complex and heterogeneous combination of soils and surfaces, ranging from well-drained loess soils dozens of feet deep to bare lava rock surfaces. The distribution of vegetation is dictated by this physiographic heterogeneity; species found growing on a lava surface differ from those found in a deep crevice in the lava surface, and both sets of species differ from species found on deep soil that might occur a few meters away. The distribution of animals also reflects the heterogeneity of their environment, both physical and floral. The impact of edaphic complexity on plant and animal distributions is enhanced by unevenly distributed sources of dispersal.

Kipuka is a name given to an area of older land surrounded by but not buried by more recent lava flows. Within the most recent lava flows on the Snake River Plain, kipukas present striking contrasts in landscapes. The approximately 150,000 ha lava surface of the Craters of the Moon Flow is about 2000–2500 years old (Prinz 1970)—recent

enough, in the cold, arid climate of southeastern Idaho, that little soil has accumulated and little vegetative colonization of the lava has taken place (Eggler 1941). Superimposed on this barren landscape are hundreds of kipukas; although these kipukas are diverse in age, edaphic and topographic characteristics, and isolation, all are well vegetated.

In the summer of 1979, I studied the distribution of plants, small mammals, and reptiles on a number of kipukas within the Craters of the Moon Flow in southeastern Idaho. This paper presents data relevant to the question, To what extent does the islandlike nature of kipukas shape the observed floral and faunal distributions?

METHODS

Study sites were located on 14 kipukas situated near the eastern edge of the Craters of the Moon Flow, 4–21 km south of Arco, Idaho (Fig. 1). The area is characterized by a continental climate, with cold winters and hot summers; mean annual precipitation, falling mostly as snow, is only about 25 cm, but it fluctuates considerably from year to year (Lovejoy 1980). The region lies within Kuchler's (1975) sagebrush-steppe vegetation zone;

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dominant shrubs are *Artemisia tridentata* (big sagebrush) and *A. tripartita* (threetip sagebrush), and dominant grasses are *Agropyron spicatum* (bluebunch wheatgrass) and *Stipa* spp. (needle-and-thread), but the importance of these and of other plant species varies broadly from kipuka to kipuka and even within kipukas.

The study kipukas range in size from 0.16 to 3.6 ha and are separated from the nearest off-lava vegetation by 70–1800 m. From one to four study plots were established on each kipuka. An effort was made to represent adequately the subjectively perceived environmental diversity on each kipuka. Slope and aspect of each plot were measured and soil character measures made.

Vegetation was sampled by canopy-cover estimation (Daubenmire 1959, Hanley 1976). Percent cover of all perennial plants was estimated for 30 0.2 by 0.5 m quadrats situated

systematically within each study plot. Species recorded during the systematic samplings were added to the comprehensive species list developed by a walking survey for each kipuka. The total plant species pool of the study area is small; fewer than 80 species on lava or kipukas were encountered during the field study, so the species lists are rather complete.

In each plot, 18 trapping stations were located 10 m apart in a 6 by 3 grid, and three Museum Special snap traps and one McGill rat trap were set at each station. Bait was peanut butter and rolled oats; after a three-day prebait period, traps were checked and reset for three or four nights. Additional traps were located in likely areas on some kipukas and in some lava areas between kipukas and the mainland. Trapping was done within a six-week period (May–June) to minimize the potential for seasonal differences in captures among kipukas (Smith et al. 1975, Johnson 1977). Lizard populations were assessed on six kipukas with unbaited pitfall traps. Lizards captured were marked and released, but marked lizards were never recaptured. Species lists of reptiles and of small mammals were augmented by personal sightings.

RESULTS

The number of plant species on the kipukas ranged from 25 to 49. The number of plants on a kipuka is significantly related to the size of the kipuka (Fig. 2), but not to the degree of isolation of the kipuka (Table 1). The prominent vegetative patterns were related to edaphic and topographic characteristics; these patterns were present within as well as among kipukas (Lovejoy 1980). A companion paper presents the results of ordinations used to explore these patterns (Carter-Lovejoy, in preparation).

Reliable assessments were made of the presence of eight species of small mammals and two lizard species on appropriately trapped kipukas. The number of lizard species on the six pitfall-trapped kipukas ranged from zero to two; species captured were *Sceloporus graciosus* (sagebrush lizard) and *Eumeces skiltonianus* (western skink). The number of small mammals on a kipuka ranged from three to seven. Four species

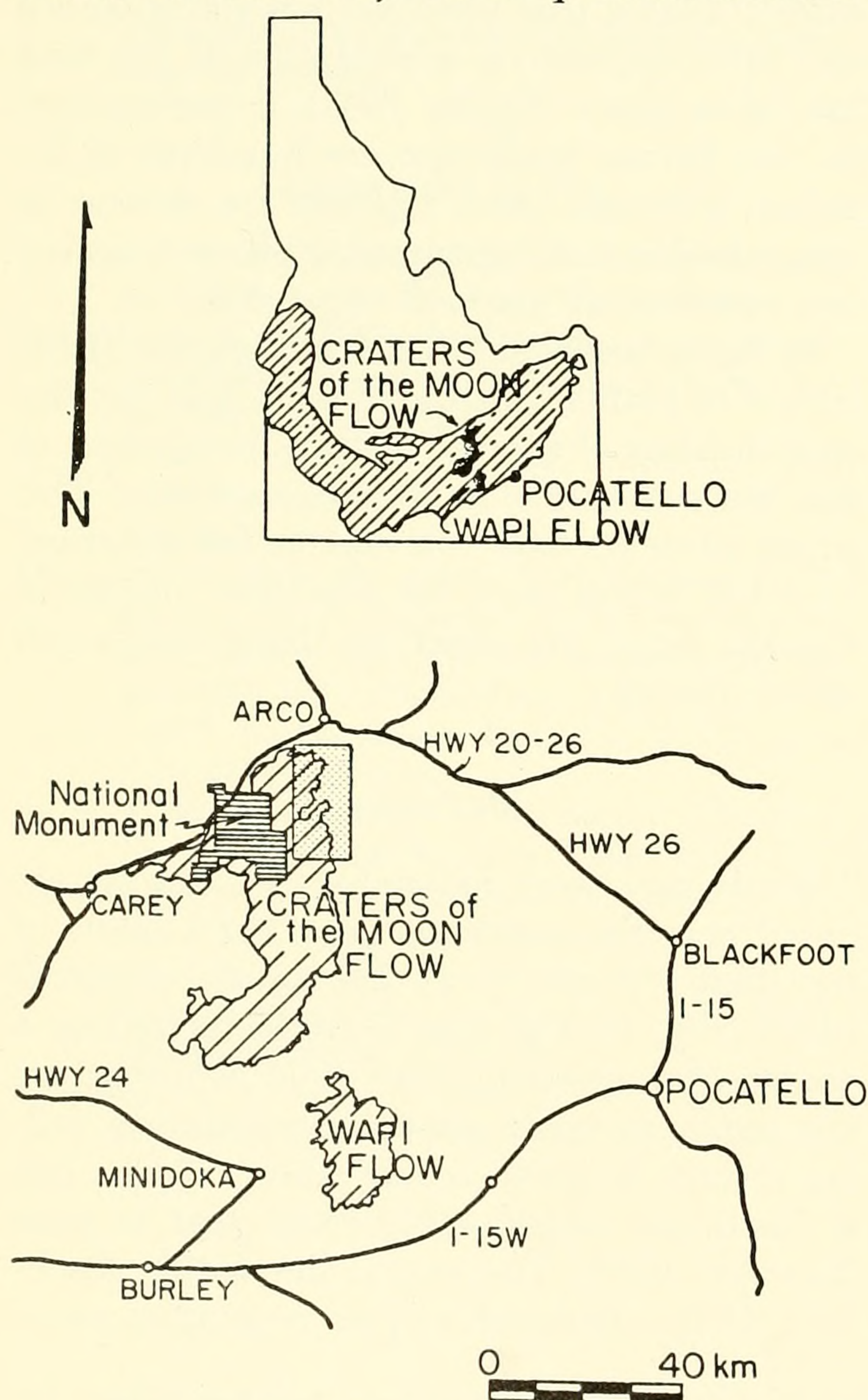


Fig. 1. a, The Snake River Plain in southern Idaho, shown with hatchmarks. b, Recent lava flows in southeastern Idaho. The study kipukas are located within the stippled area.

were widely distributed. *Peromyscus maniculatus* (white-footed deer mouse) was captured wherever traps were set, and *Eutamias minimus* (least chipmunk) was caught in most localities. As a result of their larger sizes, *Neotoma cinerea* (bushy-tailed woodrat) and *Sylvilagus nuttalli* (Nuttall's cottontail) were captured less often; however, *S. nuttalli* individuals were observed on every kipuka, and characteristic urine markings of *N. cinerea* were also ubiquitous. Four other species were captured less often: *Perognathus parvus* (Great Basin pocket mouse) was captured on two kipukas, *Microtus montanus* (montane vole) on four, *Reithrodontomys megalotis* (western harvest mouse) on one, and *Spermophilus townsendii* (Townsend's ground squirrel) was caught on three kipukas and sighted on a fourth.

As with the plant species number, the number of small mammal species on a kipuka is positively correlated with size of the kipuka (Fig. 3). The number of mammal species on a kipuka is not correlated with isolation of the kipuka, however (Table 1).

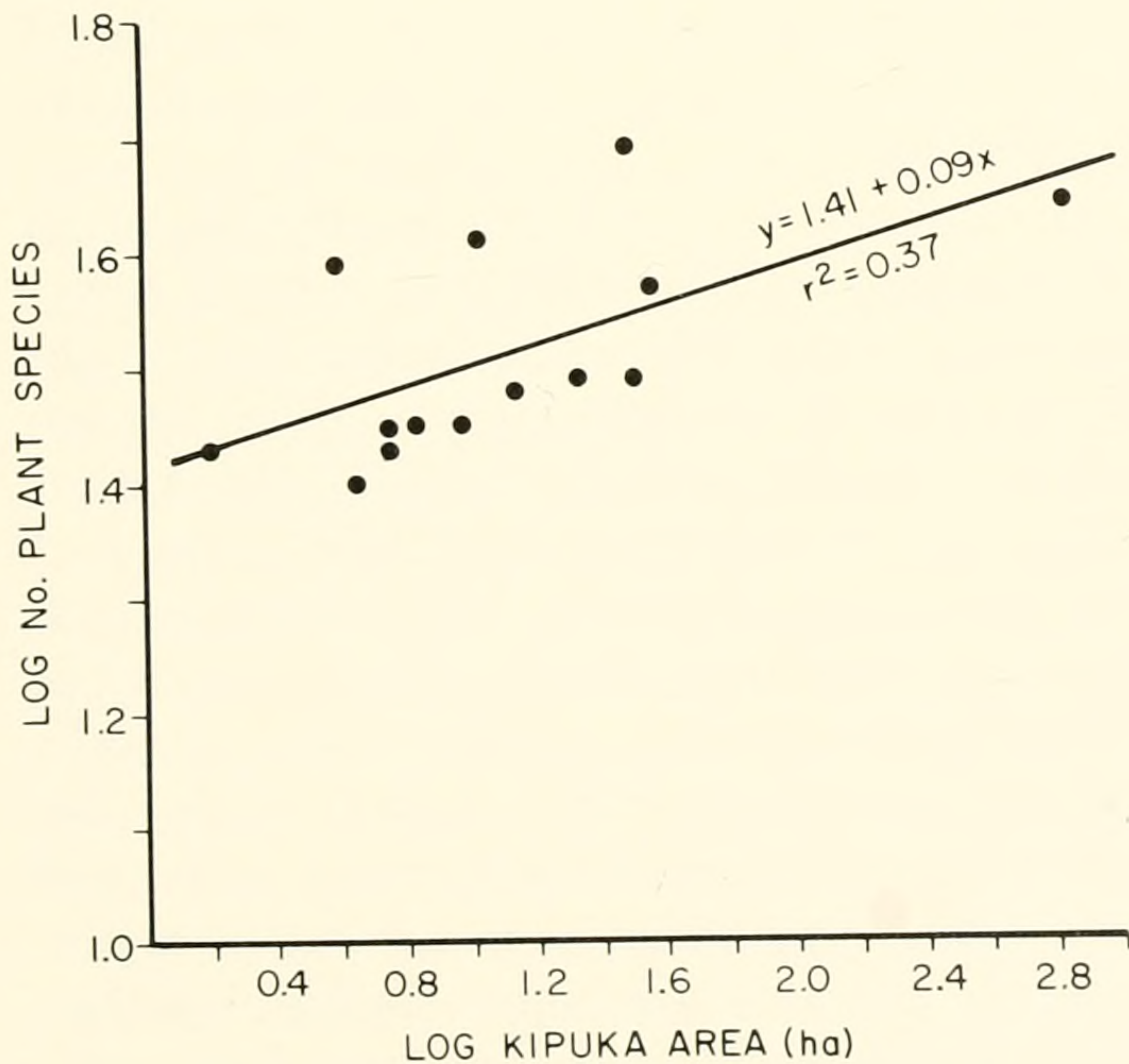


Fig. 2. Species-area effect: number of plant species on a kipuka as a function of the size of the kipuka. $P < 0.05$.

DISCUSSION

The equilibrium theory of island biogeography (MacArthur and Wilson 1967) postulates that the number of species on an island is determined by a dynamic equilibrium between immigration rate and extinction rate. The theory further maintains that two physical measures, island isolation and island size, successfully predict species immigration and extinction rates. Since its conception this theory has been widely accepted and applied by ecologists; it has recently been seriously challenged, however, for its feeble empirical support (Gilbert 1980). The equilibrium theory has been applied to several types of habitat island, often with inconsistent and poorly interpreted results (see Gilbert 1980). In this study the theory-derived prediction that more isolated kipukas have fewer species is not borne out.

Application of the MacArthur-Wilson species-isolation model has rarely been made to plants (Simberloff 1974, but see Crowe 1979). The persistence of individuals of perennial species is long relative to immigration rates. Only in systems with very broad barriers to plant dispersal or with short-lived plants dominant would the presumed isolation effect be important. Certainly Snake River Plain vegetation and the system of lava

TABLE 1. Small mammal and plant species numbers for kipukas that are grouped into size classes and arranged according to degree of isolation.

Kipuka name	Size (ha)	Distance to M.L. ^a (m)	No. mammal species ^b	No. plant species
2	.45	70	3	25
7	.16	350 ^d	5	27
4	.40	400	3	39
13	.69	550	4	28
14	.57	560	4	31
9	.57	1490	4	27
1	1.4	160	5	30
5	1.1	410	4	41
15 ^c	2.2	670	4	31
10	.97	1800	5	28
6	3.1	220	7	49
8	3.6	500	6	37
15 ^c	2.2	670	4	31
16	3.2	1270	6	31

^aDistance to mainland: shortest direct-line distance across lava.
^bNumber of small mammal species: numbers include *Neotoma cinerea* and *Sylvilagus nuttalli*, presumed present on every kipuka.
^cKipuka 15 is placed in two size classes because of its intermediate size.
^dOnly 70 m from kipuka 6.

barriers do not fit these models. Immigration of plant propagules into kipukas probably differs little from the cross-seeding that occurs among the heterogeneous habitats of the Snake River Plain.

If an isolation effect did occur, one would be more likely to observe it with small mammals; I did not observe an isolation effect. It is worthwhile to evaluate to what degree lava acts as a barrier to small mammal dispersal. *Eutamias minimus*, *P. maniculatus*, *S. nuttalli*, and *N. cinerea* were captured in traps set on lava. Scat and urine markings of the latter two species were frequently sighted up to several kilometers from any kipuka or mainland, and it is quite possible that the latter three nest and breed on lava; certainly *N. cinerea* does. Although the small amount of vegetation on the lava may limit population sizes of these four species on lava, it apparently does not restrict their ability to disperse across it.

If kipukas are not functional isolates but are, at best, the most favorable patches within a matrix of suitable habitat, then extinction on a kipuka is unlikely; indeed, in this context "extinction" has little meaning. Since individuals of these four readily dispersing species made up over 96 percent of all small

mammal captures, examination of aggregate small mammal data should obviously reveal no isolation effect.

It is much less likely that the four other small mammal species trapped here actually reside on lava. One *M. montanus* individual was sighted one night on lava less than 50 m from both a kipuka and the mainland; in no other instance were any of these species sighted or captured on lava. On the other hand, they were not very commonly sighted on kipukas either. Only 24 individuals of these four species were captured. Given the high trapping intensity on kipukas, it is possible to assume that individuals representing the sole capture of their species on any kipuka are immigrants to the kipuka, not members of established populations. There were 11 encounters of these four species during the study; in only 4 cases were we sampling a population (conservatively defined as two or more individuals). The other 7 encounters were of single individuals, despite exhaustive trapping of the habitats in which these individuals were found.

Isolation seemed to play no role in the presence of the two lizard species found on the kipukas either. On the other hand, on no kipuka did we find the diurnal and conspicuous *Phrynosoma douglassi* (desert short-horned lizard), even though it was frequently sighted on mainland; its total absence on kipukas suggests that lava is more of a barrier to the dispersal of this slow-moving lizard than it is to the dispersal of the two quicker species.

One interesting and unexpected isolation effect does exist: the density of animals is significantly and positively correlated with isolation (Fig. 4). Common explanations for so-called "density compensation" (MacArthur 1972) are not appropriate in light of the fact that the density measure, individuals per 100 trap nights, reflects changes in the density of the common species, to which lava is not a barrier. One possible mechanism for increased density on isolated kipukas is reduced predation. Densities of prey for common predators in the area are higher on kipukas than they are on nearby lava, because of the relative abundance of vegetation on kipukas. As a result of this concentration of prey, predators are likely to focus their attention on

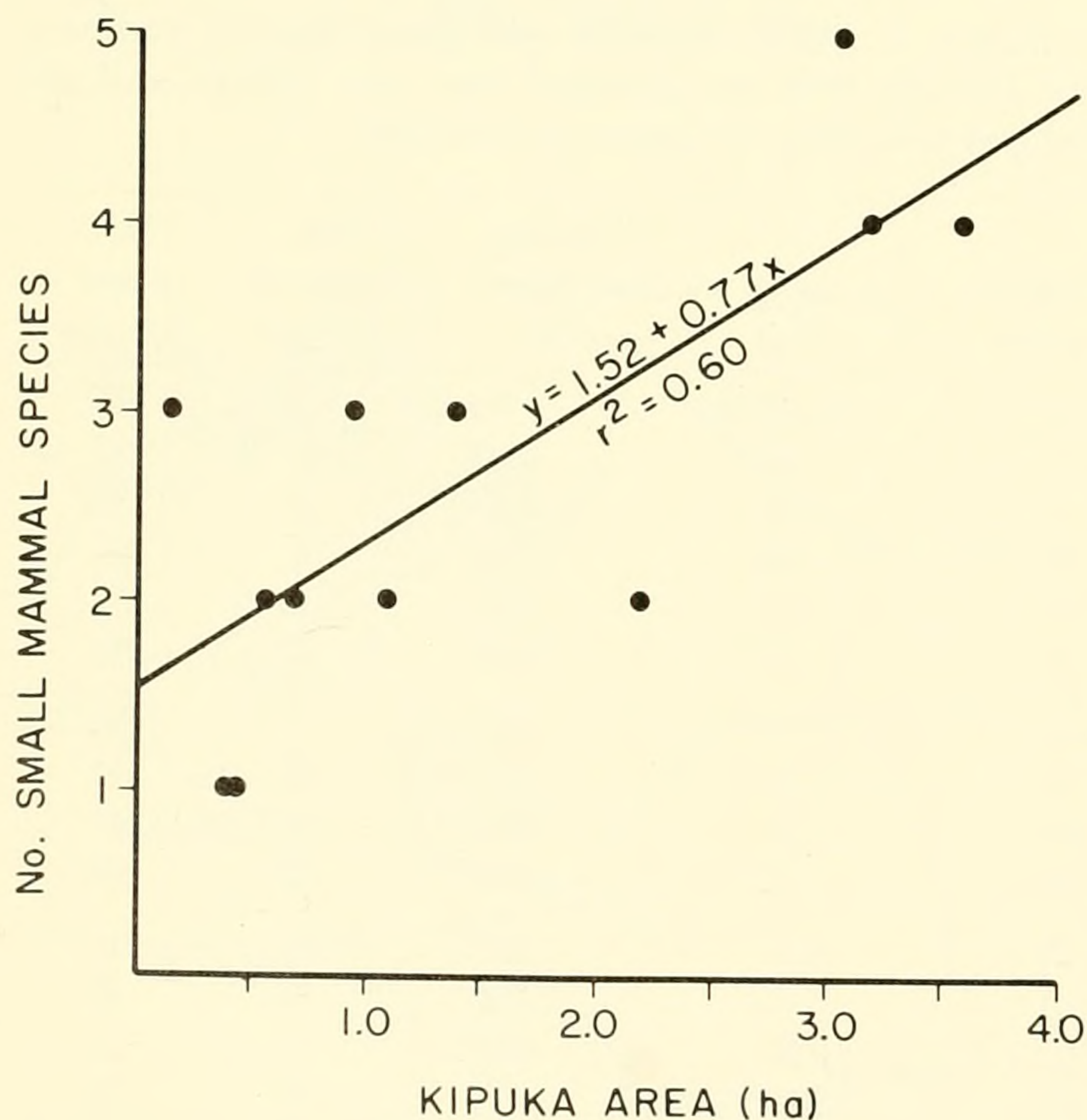


Fig. 3. Species-area effect: number of small mammal species on a kipuka as a function of the size of the kipuka. $P < 0.01$.

kipukas. Predation pressure is intermittent, however, particularly on smaller kipukas. Small kipukas (less than 3 ha) are probably not large enough to support a snake population (Lovejoy 1980). We rarely observed birds of prey over the study area, perhaps because of the lack of roosts. Although scat finds indicated that coyotes were occasional visitors to all study kipukas, none of the kipukas is large enough to support a resident coyote. So, between times of possibly intense predation, kipukas may enjoy periods of total release from predation pressure. During these lulls, small mammal populations may be able to build up to densities that greatly exceed densities on less isolated kipukas, where predators may forage more frequently. Certainly this density-isolation phenomenon deserves further study.

Connor and McCoy (1979) discuss three mechanisms that can explain an observed species-area effect. The "habitat-diversity" hypothesis (Williams 1964) postulates that, as increasingly larger areas are sampled, new habitats with associated new species are encountered. According to the "area-per se" hypothesis (Preston 1960, MacArthur and Wilson 1967), population sizes are proportionately smaller on smaller isolates, implying increased probability of species extinctions. An alternative "passive sampling" hypothesis (Connor and McCoy 1979) holds that species number is controlled by passive sampling from a species pool, so that larger areas intercept larger samples than smaller areas. Connor and McCoy consider this a good "null" hypothesis.

The area-per se hypothesis is associated with the equilibrium island biogeography model; the implication is that an ecologically significant rate of species extinction results in a turnover of species. A number of studies (Gilbert 1980:214, cites 23) purport to support the equilibrium model by demonstrating species-area relationships among island groupings, despite the fact that an observation of a species-area relationship made in a temporally limited study cannot demonstrate species turnover and thus cannot distinguish between the three causal hypotheses above. Specific manipulative experimentation is necessary to distinguish among these hypotheses; unfortunately, such experimentation is

virtually nonexistent. Without such experimentation, one can only speculate about causes for the observed relationship.

Data from this study could be used to support all three hypotheses, without refuting any of them. Certainly environmental heterogeneity increases with increasing kipuka size, because larger kipukas have more topographic variation. Support for the null hypothesis can be noted by looking strictly at the numbers of small mammal immigrants on kipukas of different sizes (Fig. 5). These immigrants have presumably reached the kipukas on which they were found by chance; nevertheless, they show a species-area effect, indicating the kipukas are passively sampling small mammal dispersers.

The area-per se hypothesis also appears to have some application to these data. Perhaps the most intrinsically acceptable explanation for the species-area relationship lies with the population ecology of the different species contributing to species number. Equilibrium theory's contention that extinction rates decline with increasing area is by no means certain; on the other hand, decreasing area will at some point result in the extinction of any

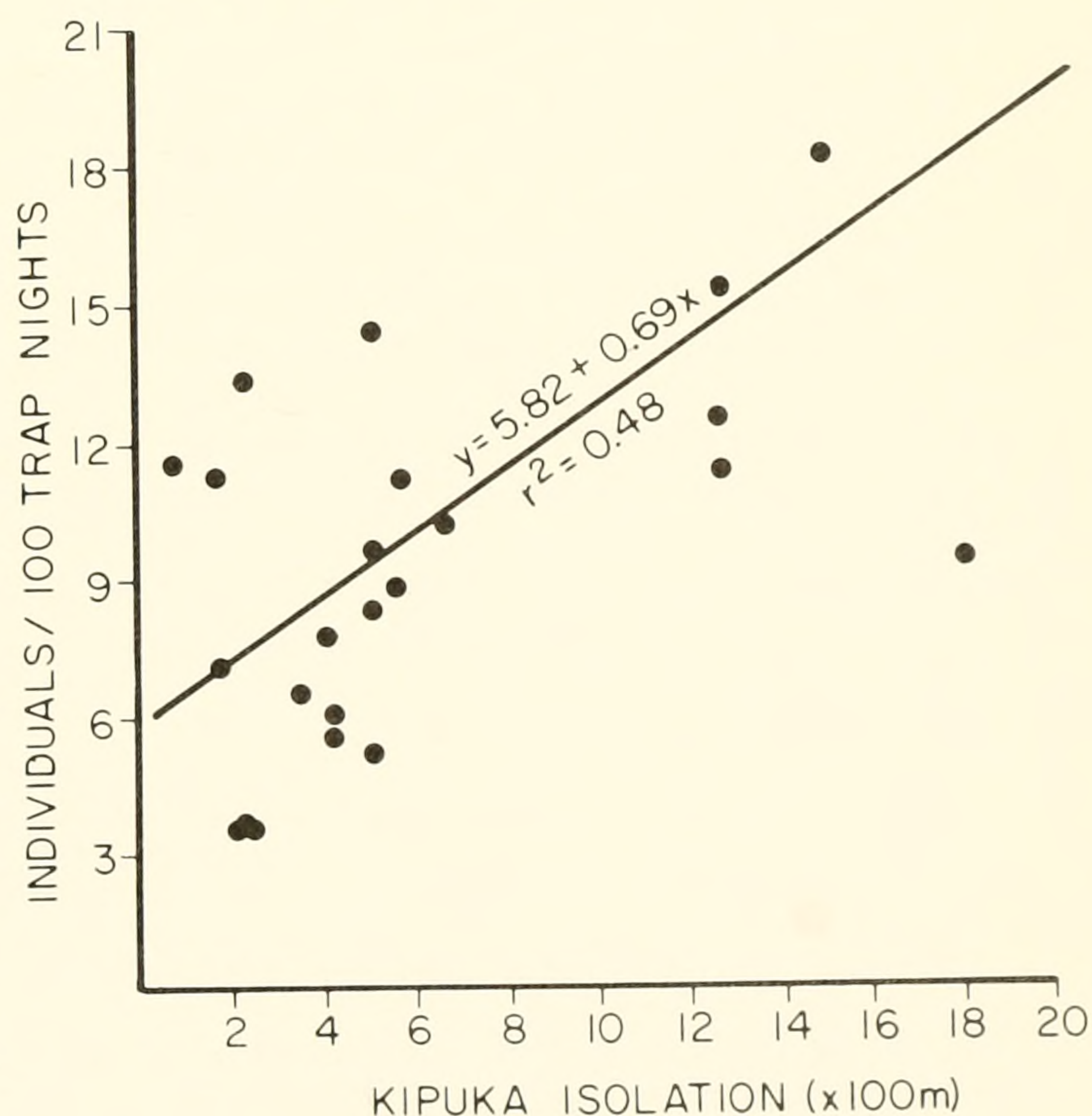


Fig. 4. Density-isolation effect: small mammal density (number of individuals captured for every 100 nights of trapping) as a function of kipuka isolation (straight-line distance to nearest mainland). $P < 0.05$.

particular population. Thus, there must exist some threshold size for each species, below which the probability of extinction of a population of this species is one (Shaffer 1981). Of the small mammal species observed on kipukas for which lava poses an impediment to dispersal, three species appear to have had established populations on at least one kipuka: *P. parvus*, *S. townsendii*, and *M. montanus*. None of these populations was on a kipuka less than three ha in size (Fig. 5). The species involved did not appear to be restricted to a particular type of habitat that was unavailable on smaller kipukas, nor did the increase in environmental heterogeneity on kipukas of larger size appear to be important to the individual species. Instead, it is possible that these species need an area of at least three hectares in this ecosystem to support a large enough number of individuals to maintain a population. Perhaps those species that did not have populations on any of the study kipukas have minimum area requirements larger than three ha.

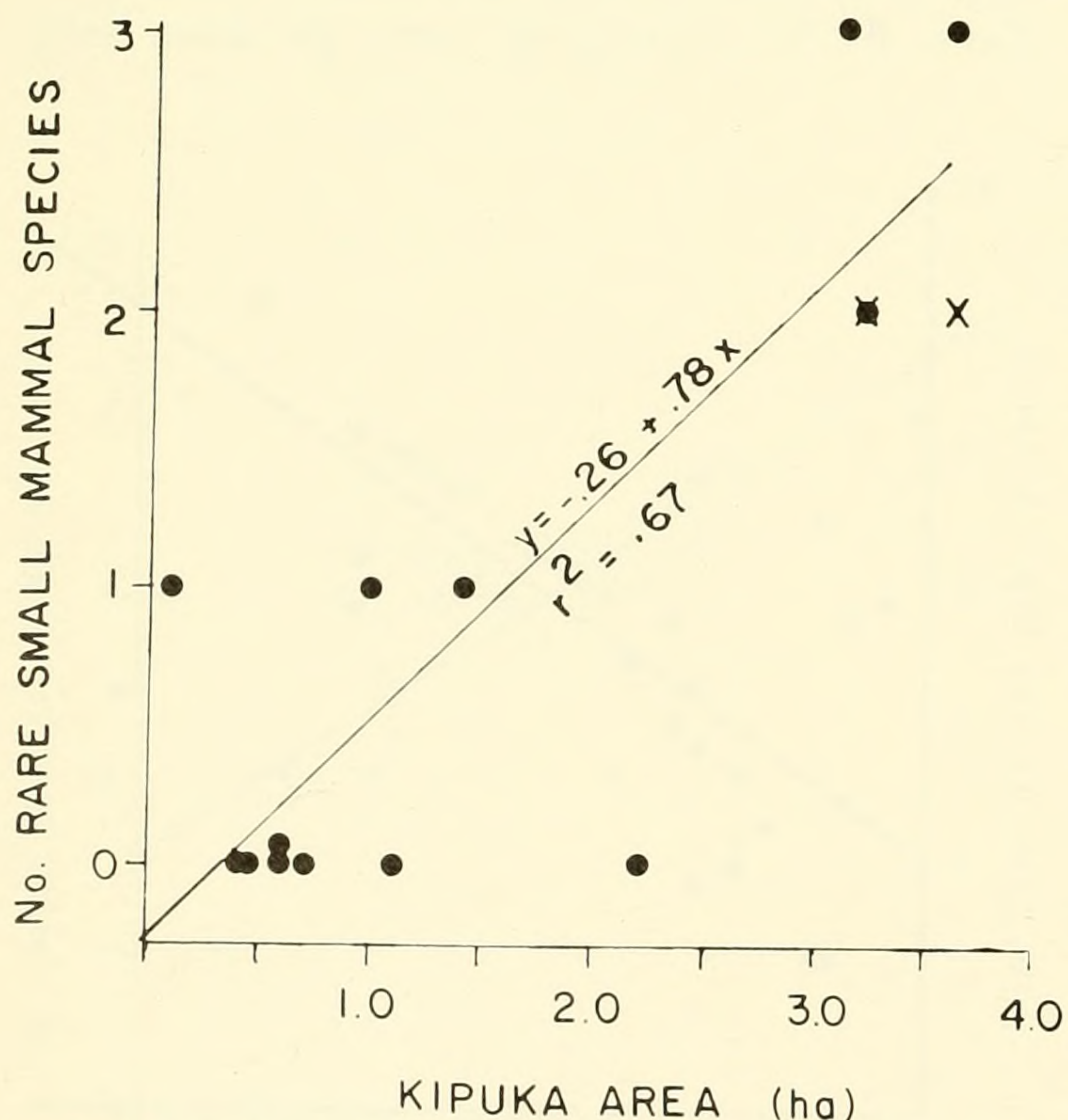


Fig. 5. Species-area effect: number of rare small mammal species on a kipuka as a function of kipuka size. Dots indicate number of species with one or more individuals; X's indicate number of species with two or more individuals. Species considered rare are *P. parvus*, *S. townsendii*, *M. montanus*, and *R. megalotis*. $P < 0.001$.

The minimum size requirements of many species relate to energetics and the available food resource (McNab 1963, Harestad and Bunnell 1979). Species vary in the amount of food required for living and reproducing: larger animals require more food, as do metabolically more active animals. This might account for the absence of *Lepus californicus* (blacktail jackrabbit) and *Dipodomys ordii* (Ord's kangaroo rat) from all study kipukas, even though both species were common on nearby off-lava sites. Animals at higher positions in community trophic structures require more cumulative biomass to stay alive, and populations of such animals will require larger areas in which individuals can forage for food. The absence of the carnivorous (*Onychomys leucogaster* (grasshopper mouse) might be explained by this reasoning. Snakes—*Coluber constrictor* (racer), *Crotalus viridis* (Great Basin rattlesnake), and *Pituophis melanoleucus* (Great Basin gopher snake)—were sighted only on those kipukas or kipuka archipelagos that are greater than three ha in size.

Social behavior is another factor that plays a role in the determination of minimum area requirements, although social behavior is, of course, largely an evolutionary response to energetic considerations. The home range of an animal is an expression of both the social and energetic factors, so that home range sizes, when known, are a rough indication of relative minimum size requirements for small mammals. Literature values for the home range sizes of two mainland species not found on kipukas (1.3–1.4 ha for *O. leucogaster*, 2.7–4.6 ha for *D. ordii* [French et al. 1975]) are considerably larger than those for kipuka-dwelling *P. parvus* (.05–.4 ha [O'Farrell et al. 1975]).

Of course, alternative explanations exist for the absence of the small mammal species that were not found. There might be a lack of suitable habitat on kipukas for some species; for instance, *D. ordii* is generally associated with sandy soils, and only one trapped kipuka met this criterion. If the missing species was absent as well from the mainland immediately adjacent to the lava flow, there would be no ready source of immigrants to colonize kipukas. Lava is probably a very effective,

perhaps impenetrable barrier to some species. Certainly the observed distribution of small mammal species can be explained, not through any grand mechanism, but through the agglomerative contributions of a variety of population and community functions. The best understanding of patterns of distribution in the kipuka-lava ecosystem will primarily be elaborated, in the future, by autecological research.

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