Habitat Selection, Interspecific Competition, and Coexistence of a Habitat Generalist and Specialist in Temperate Rainforest of Southeastern Alaska

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Abstract

Communities include habitat generalists whose resource use overlaps specialists. Habitat selection is a mechanism that allows competing species to coexist. Interspecific competition can facilitate coexistence directly or through promoting differential habitat selection. Habitat selection and interspecific competition can vary with population density; however, their roles in determining relative abundance of species across habitat space are poorly understood. We studied *Peromyscus keeni*, which flourishes in a range of habitats in southeastern Alaska, and *Myodes gapperi*, a specialist of mature coniferous forests in western North America, to elucidate how these mechanisms may facilitate coexistence in temperate rainforest. We used stepwise multiple regressions of minimum known alive (standardized to unit variance) across 1 ha grids during spring 1999–2000 and autumn 1998–2000 to determine contributions each variable, in each significant regression model, made to the variance in abundance for each species. We determined relative contributions of interspecific competition versus habitat selection in explaining species' habitat use among four different types of rainforest habitat. Intensity of interspecific competition (both directions) varied with population density and season. Habitat variables, rather than interspecific competition, explained variation in species' abundance at population peaks when intraspecific competition would be intense. Interspecific competition, with habitat, was significant at all other times. Our findings suggest habitat selection and interspecific competition explain variation in the abundance of both species among habitats, but contributions vary seasonally and with density. During spring, interspecific competition seemingly plays a greater role at higher densities, but during autumn interspecific competition increases its relative contribution as population density decreases.

Keywords: *Myodes gapperi, Peromyscus keeni*, coexistence, interspecific competition, temperate rainforest

Introduction

Differential habitat selection is the primary means for members of ecological communities to coexist (Schoener 1974a; Rosenzweig 1981, 1989; Hallett 1982; Bonesi and Macdonald 2004). Still, communities often include generalists whose resource use overlaps that of specialists (e.g., Miller 1964). Habitat generalists coexist with specialists by exploiting underutilized habitat space (Morris 1996). Nonetheless, many studies suggest that microhabitat selection is an important determinant of community structure (Rosenzweig 1989) and that the principal mechanism driving differential microhabitat selection is interspecific competition (Schoener 1974a). Much of the empirical foundation comes from studies of small mammals (Grant 1972, 1978, Rosenzweig 1981, Eccard and Ylonen 2003, Eccard et al. 2011).

Recognition that small mammal species respond to specific components of their environment on a scale of resolution much finer than gross habitat differences (MacArthur and Pianka 1966) led to studies of microhabitat partitioning and interspecific competition (Rosenzweig and Winakur 1969). This new knowledge and subsequent availability of multivariate statistical procedures prompted detailed ecological studies of microhabitat selection (M'Closkey 1976, Dueser and Shugart 1978, Morris 1987a). Studies of habitat selection by small mammals have revealed complex relation-

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ships between habitat heterogeneity and species coexistence, resource partitioning, and competition among syntopic populations (Morris et al. 2000, Lin and Batzli 2001, Fletcher 2007, Falcy and Danielson 2013). Individuals choose habitats in which reproductive success is optimized (MacArthur and Pianka 1966). This decision depends on the basic suitability of different habitats, discounted by the density-dependent demands of the existing population (Rosenzweig and Abramsky 1985, Morris 1987b) and further modified by interspecific interactions (Schoener 1974b, Crowell and Pimm 1976). However, empirical support for the contributions of various ecological factors in facilitating coexistence among small mammals has been inconclusive because studies of habitat selection often can be confounded by spatial autocorrelation (Falcy and Danielson 2013) and because a direct measure of interspecific competition was largely unavailable (Hallett and Pimm 1975).

A technique for direct estimation of competition coefficients using multiple regression analysis to separate the effects of habitat selection from interspecific competition was developed as the Schoener-Pimm technique (Schoener 1974b, Crowell and Pimm 1976, Hallett 1982, Hallett et al. 1983). However, concerns about an artifact in this approach (Rosenzweig et al. 1985) led to other methods of assessing the role of habitat selection (isoleg theory—Morris 1989; Rosenzweig 1989, 1991; isodars—Morris 1987, 1988). A methodological artefact was confirmed while studying the Schoener-Pimm regression technique (Fox and Luo 1996); however, they discovered and demonstrated experimentally that if census data are normally standardized (i.e., standardized to unit variance = [x_i − $\bar{x}$]/SD), then the technique works well. This modified technique was rigorously tested using results from previous experimental removal manipulations (Higgs and Fox 1993, Thompson and Fox 1993) and subsequently used to demonstrate competitive interactions among rodents in a temperate, wet sclerophyll forest in Tasmania (Luo et al. 1998). So as evidenced by the foregoing, we propose empirical data provide clear resolution of alternative explanations of species occurrences resulting from interspecific competition and habitat selection as opposed to random distributions.

In southeastern Alaska, Smith and Nichols (2004) studied Keen's mouse (*Peromyscus keeni*), an apparent habitat generalist in coastal, temperate rainforests (Van Horne 1981, 1982a; Hanley and Barnard 1999), and the red-backed vole (*Myodes gapperi*), a reputed specialist of mesic–wet, mature forests (Morris 1996, Sullivan et al. 2000, Hodson et al. 2010), to quantify demographic attributes among undisturbed and recently logged habitat types. Smith et al. (2005) analyzed captures among habitat types and at trap stations (i.e., microhabitats) within habitat types during spring and autumn to quantify habitat relations of each species, providing insights into how cumulative broad-scale disturbance might influence mouse and vole persistence across landscapes. The study included samples from spring and autumn because of expected seasonal differences in the age structure and density of populations (Van Horne 1981, 1982; Smith and Nichols 2004; Eccard et al. 2011) and in the diversity and abundance of key food resources (e.g., fungi; Flaherty et al. 2010). Live-trap census data from a replicated experiment in 1998–2000 in four habitat types revealed patterns of density-dependent habitat distribution and microhabitat use among gap-phase old growth (OG), wind-originated old growth (WO), precommercially thinned young growth (SG), and peatland mixed-conifer forests (MC). Correlates of habitat use varied with spatial scale, between seasons, and among habitats, with < 10% of the explained variation attributable to spatial autocorrelation. Habitat distribution and microhabitat use varied with density, especially for voles, which at lower densities became more selective, using fewer habitat types and microhabitats. Conversely, mouse habitat use was influenced less by population density and was less selective at both spatial scales, as evidenced by a more uniform distribution among habitat types and fewer significant models of microhabitat use (Smith et al. 2005).

However, 62% of the variation in mouse density among habitat types was attributed to vole density. Furthermore, mouse captures during spring (when food resources are relatively scarce; Flaherty et al. 2010) were most influenced by microhabitat use by voles in selected habitat types, with the recent capture of a vole increasing the odds of mouse capture in OG by 28% while decreasing the odds of mouse capture in WO by 29% (Smith et al. 2005). These findings underscore the potential for overlap in habitat use between mice and voles (Morris 1996) and the influence of density-dependent behaviors on animal distribution across habitats (Hodson et al. 2010), and further suggest that although habitat explains significant variation in the microhabitat use of these two species, interspecific interactions might also play a significant role in their distribution and relative abundance among habitat types.

Voles are constrained to wetter environments because of their physiological requirement for water (10 × that of mice; Getz 1968), and thus voles compete for mesic–wet habitat space (Getz 1968). Mice on the other hand are probably seeking habitat space with less intraspecific competition (Miller 1964, Fretwell and Lucas 1970, Morris 1996, Hodson et al. 2010). Coexistence can occur between two species with similar ecologies if the specialist is able to competitively exclude the generalist in portions of at least one niche dimension (habitat, food, etc.) where it has evolved to be superior (Miller 1964, Morris 1996). In conditions such as in southeastern Alaska, where mice essentially flourish everywhere and voles are old growth reliant (Smith and Nichols 2004, Smith et al. 2005), voles are most competitive in portions of the landscape that represent their optimum habitat (OG). Mice that are able to exploit OG, especially when intraspecific competition is intense, should realize higher fitness than individuals that remain in overexploited habitats (Fretwell and Lucas 1970, Morris 1996, Hodson et al. 2010).

The purpose of this paper is to further examine factors facilitating the coexistence of *M. gapperi* and *P. keeni* in southeastern Alaska by discerning the relative contributions of habitat selection and interspecific competition in explaining the variation in relative abundances of these two species among four common rainforest habitats. We examined the following questions:

1. What is the relative importance of microhabitat selection and interspecific competition in explaining the relative abundance of voles and mice?
2. Do the contributions of microhabitat selection and interspecific competition between voles and mice vary among different habitat types?
3. Do the contributions of microhabitat selection and interspecific competition between voles and mice vary between spring and autumn?
4. How does the relative importance of interspecific competition and microhabitat selection vary with population density of either species?

We use the modified Schoener-Pimm technique, with a normal standardization of census data from an earlier companion study (Smith and Nichols 2004), to discern level of interspecific competition between voles and mice from microhabitat variables, and determine the relative importance of competition and habitat selection in facilitating coexistence within rainforests of southeastern Alaska.

Methods

Study Area

The study sites were on Wrangell Island (56° 30’ N, 132° 17’ W), a near-shore island ~ 500 km^2 in area with elevation ranging from sea level to 853 m (Smith and Nichols 2004). Across the region, temperate coniferous rainforest dominates the landscape up to 600 m elevation, with about 90% in old-growth Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forests; remaining areas are alpine, muskeg (sparsely-forested peatland) or riparian (Harris and Farr 1974). About 50% of Wrangell Island was productive (> 75m^3/ha merchantable timber; Julin and Caouette 1997) forestland, of which about 11% was clearcut-logged during the previous four decades. The two productive old-growth habitats were forests with contrasting disturbance regimes and notable differences in canopy, understory, and stand structure (Nowacki and Kramer 1998, Smith et al. 2005). OG usually occurs on slopes sheltered from prevailing windstorms and experiences frequent, less intense disturbance that results in blowdowns of one to a few trees (Kramer et al. 2001). This habitat is relatively homogeneous at the scale of < 1 ha (Smith et al. 2005), with fine scale spatial heterogeneity resulting from canopy gaps, the majority of which are < 50m^2 in area (Nowacki and Kramer 1998); trees are typically > 400 years old. In contrast, wind-originated old growth (WO) typically has a southerly exposure and experiences infrequent (100–200 years), catastrophic disturbance from windstorms that often blow down 10–100 ha of forest (Nowacki and Kramer 1998, Kramer et al. 2001). This habitat is spatially heterogeneous at a broader scale (weighted mean = 11 ha), with uniform diameter trees (typically 100–200 years old) distributed throughout the stand; trees are rarely > 300 years old.

The overstory of old-growth forest is comprised mostly of Sitka spruce and western hemlock. Wetter sites include a larger component of western redcedar (*Thuja plicata*) or yellow-cedar (*Chamaecyparis nootkatensis*) in the canopy. Large trees (> 74 cm diameter), downed and decaying wood, snags, and heterogeneous substrates are key components of these habitats. The understory is dominated by blueberry (*Vaccinium* spp.), especially in canopy gaps (Ver Hoef et al. 1988, Hanley and Brady 1997). Because of a more uniformly closed canopy, wind-originated stands have sparser understory vegetation than gap-phase forest (Smith et al. 2005). In contrast, peatland mixed-conifer sites are typified by poor drainage and shallow, organic soils with patches of more productive mixed-conifer forests that occur on elevated sites of deeper mineral soils (Neiland 1971). Conifer vegetation varies from mostly lodgepole pine (*Pinus contorta*), which occurs as an open canopy, scrub forest in muskegs, to more productive mixed-conifer forest of lodgepole pine, yellow-cedar, redcedar, western hemlock, and mountain hemlock (*Tsuga mertensiana*). Understory vegetation varies considerably (Alaback 1982) with open areas dominated by a mixture of sedges (*Carex* spp.), grasses (Poaceae), skunk cabbage (*Lysichiton americanum*), and Labrador tea (*Ledum glandulosum*). Blueberry dominates the understory of sites with well-developed overstories (Smith et al. 2005).

Study Species

We studied two common small mammals of coastal temperate rainforest (MacDonald and Cook 1996, Smith et al. 2001, Smith and Nichols 2004). The red-backed vole (*M. gapperi*) ranges across northern North America and is common in mature mesic forest habitats in the Hudsonian and Canadian life zones (Merritt 1981). In southeastern Alaska, there are four endemic subspecies (Runck and Cook 2005); we studied *M. g. wrangeli*, which is known from three islands (MacDonald and Cook 1996). Keen's mouse (*P. keeni*) is a sibling species of the ubiquitous *P. maniculatus* and occurs as three island endemic subspecies and two subspecies with ranges largely restricted to southeastern Alaska (Hogan et al. 1993, MacDonald and Cook 1996). It occurs in riparian and upland old-growth forests, fens, and regenerating second-growth forests (Smith et al. 2005) throughout southeastern Alaska; its range extends south along the coast of British Columbia to the Olympic Peninsula of Washington (Hogan et al. 1993).

Voles and mice in our study area were similar in size during both seasons. During spring, mean body mass (± 95% confidence coefficient) of voles and mice were 22.5 (1.84) g and 23.8 (0.99) g, respectively. Corresponding autumn values were 25.5 (1.47) g and 25.5 (1.40) g. Variation (CV < 10%) existed between seasons and among habitats and years, but patterns were similar for both species as 95% confidence intervals overlapped in all comparisons. Body length (total length–tail length) of voles (94.9 ± 1.8 mm) and mice (94.1 ± 1.7 mm) were also similar.

Sampling Small Mammals

Six (Two replicates of OG, WO, and MC) 1 ha (100 m × 100 m) grids in unmanaged landscapes and two 1 ha grids in SG stands in an intensively logged (47% early seral forests) watershed were live trapped to estimate mouse and vole abundance and habitat relations (Smith and Nichols 2004). Both logged sites were 23-yr-old second-growth stands thinned to a spacing of 5.5 m (± 25%) during spring 1996. Study sites were replicates of four habitats selected according to type and frequency of disturbance, overstory cover, and management history. Replicates of each habitat type were located in the same watershed to minimize geographical variation, but ≥ 800 m apart to achieve independence. All grids were an 11 x 11 array of trap stations at 10 m intervals with two Sherman live traps (H. B. Sherman, Tallahassee, FL) per station. Except for MC, which was not sampled in 1998, sites were live-trapped during spring and autumn 1998–2000 for 3–4 consecutive nights. Captures were uniquely toe-clipped (Smith and Nichols 2004) and released at the capture location. No animals were sacrificed during the study. Minimum number of animals known to be alive (MNA; Krebs 1966) was computed from the history of captures on each grid (Smith and Nichols 2004). Population density ($\hat{D}$) was determined with a Lincoln-Petersen estimate of population size (Smith and Nichols 2004) and an estimate of effective area sampled (Van Horne 1982b).

Sampling Habitat

Shortly after live trapping was completed each season, 26 vegetative and structural microhabitat elements were measured using two nested plots at trap stations where voles or mice were captured (Smith et al. 2005). Microhabitat elements included understory vegetation, dead (i.e., snags) and live standing trees, and volume and decay class (Fogel et al. 1973) of downed woody material. Understory microhabitat variables were visually estimated (percent cover) in 1 x 1 m subplots placed at the trap station and at distances of 4 m and 7 m from the trap station in each of the four cardinal directions (nine subplots/station). Within each subplot, percent cover (to the nearest 5%) of herbaceous vegetation, moss, woody debris (< 25 cm in diameter), and water were measured (Smith et al. 2005). Percent cover of three groups of woody vegetation in each of two vertical strata: < 30 cm and 30–150 cm also were recorded. The three groups were: 1) *Vaccinium*, of which the most common species were red huckleberry (*V. parvifolium*) and two species of blueberry (*V. alaskaense* and *V. ovalifolium*); 2) all other deciduous species; and 3) conifer species, primarily western hemlock, mountain hemlock, and Sitka spruce. *Vaccinium* was separated from other deciduous species because it is commonly the dominant understory woody vegetation in southeastern Alaska (Hanley and Brady 1997). Mean values of the nine subplots were used to describe the understory at each trap station.

Density of live trees and snags was calculated for all plant species pooled (Smith et al. 2005). Snags were defined as a standing dead tree > 10 cm diameter at breast height (dbh) and > 1.5 m tall (Spies et al. 1988). Snags were classified as hard snags, which were dead trees with > 2% of their limbs > 30 cm in length remaining, and soft snags, which were snags with < 2% of their limbs > 30 cm in length remaining (Rosenberg and Anthony 1992). Live and dead trees were counted within a circular 12.6 m or 20 m radius plot centered at the trap station, depending upon the dbh of trees. Within a 12.6 m radius, number of live trees in each of two dbh categories (5–10 cm, 11–49 cm) and number of hard and soft snags 10–49 cm in bole diameter were recorded. Within a 20 m radius, number of live trees and snags in each of two classes of larger trees: 50–73 cm, and > 74 cm were recorded. Similarly, volume of downed wood in each decay class was estimated in either 12.6 m or 20 m radius of the trap station (Smith et al. 2005). For each piece of downed wood, midpoint diameter (cm), decay class (I–V), and length were recorded; length and circumference were used to calculate volume and decay status was determined for woody material > 10 cm diameter (Sollins 1982). Similarly, volume of downed wood was recorded (Smith et al. 2005), segregated by decay class, which included criteria of the presence of live vegetation, moss, or seed sprouts, structural integrity of the wood, number of limbs remaining, and overall structure in the context of the forest floor (i.e., above forest floor, slightly covered with moss, or indistinguishable from forest floor). All downed wood 25–50 cm (midpoint diameter) was counted in a 12.6 m radius plot, whereas larger pieces (> 50 cm) were counted in a 20 m radius plot. Amount of downed wood for each trap station was estimated as volume (m^3) per m^2 (Smith et al. 2005).

Analyses

We used MNA and $\hat{D}$ estimates for each combination of habitat type, season, and year. Each was used where it was most appropriate: $\hat{D}$ (computed for effective areas an order of magnitude greater than the grids) was used to estimate relative abundance of each species among habitat types; MNA (computed from captures at individual trap station) was used to examine interspecific interactions at the scale of microhabitats. Also, we compiled the number of captures, the number of trap stations where each species was recorded exclusively, the number of trap stations where both species were captured, and the number of stations where neither was captured. For each species, we compared those statistics to corresponding estimates of $\hat{D}$ to assess the extent to which habitat space and habitat selectivity varied for each species relative to its own population size and the population size of the second species. Because there were two traps per station and few instances (< 1%) when empty traps were nonfunctional, stations with one capture almost always had another trap available to capture a second individual.

From a total of 968 trap stations (726 during 1998), the data set for each regression analysis was determined by identifying and recording all captures at all trap stations for which either or both species were captured for each year and season trapping session. MNA (Krebs 1966) was calculated and used to estimate the local abundance of each species. Microhabitat data were measured for all trap stations for which captures were recorded. Hence, each regression analysis had a unique data set for that analysis. This technique allowed us to better analyze abundance of each species relative to habitat variables measured at corresponding trap stations. When examining patterns in time we used density estimates ($\hat{D}$) from Smith and Nichols (2004) to illustrate patterns without a confounding bias of effective area sampled (Van Horne 1982b).

To reduce collinearity, we conducted a multiple correlation analysis for each data set and eliminated habitat variables deemed to be too correlated ($r \geq 0.7$) for inclusion. From the total of 26 habitat variables measured (Smith et al. 2005), 19 variables were included as independent variables in preliminary regression analyses. From those regression analyses, a subset of 14 variables was selected as meeting the criteria that the variable had been included in ≥ 1 significant regression equation. Hence, this same set of 14 habitat variables plus abundance (MNA) measures for each of the two species were used in all subsequent stepwise regression analyses. For each year/season analysis, the two replicate sites from each habitat type were all pooled into one unique data set for that year/season, as there were no significant differences between paired replicate sites. To avoid any statistical artefact (Fox and Luo 1996), the number of unique animals of each species (MNA) captured at each station for each unique data set was standardized to unit variance (hereafter standardized) according to the equation $[x_i - \bar{x}]/\mathrm{SD}$ before these values were entered into a regression. A separate analysis was conducted for each season in each of the three years. To analyze each habitat separately, each of the above data sets (season/year) was stratified according to habitat and MNA values for both species were standardized for each year/season/habitat data set.

We used forward stepwise multiple regression in Statview 5.0 (SAS 1992–98) with $F = 2.00$ for variables to enter the model, following the protocols described in Rosenzweig et al. (1985) and Fox and Luo (1996). The two regression equations of interest here are:

$$Y\mathrm{mj} = a + bpX\mathrm{pj} + b1X1\mathrm{j} + b2X2\mathrm{j} + \ldots + bzXz\mathrm{j} \qquad (1)$$

$$Y\mathrm{pj} = a + bmX\mathrm{mj} + \mathrm{b1X1j} + b2X2\mathrm{j} + \ldots + bzXz\mathrm{j} \qquad (2)$$

where,

Ymj = standardized MNA of *M. gapperi* at station j;

Ypj = standardized MNA of *P. keeni* at station j;

Xmj = standardized MNA of *M. gapperi* at station j;

Xpj = standardized MNA of *P. keeni* at station j;

Xij = value of the ith habitat variable at station j;

i = 1 to z where z is the number of habitat variables included in the model;

a, *b*p, *b*m, *b*1, *b*2, … , *bz* are regression coefficients.

The dependent variable for *M. gapperi* was Y_{mj} (the standardized MNA of *M. gapperi* at trap station j) and the standardized regression coefficient (b_{p}) of the second species, *P. keeni*, as an independent variable in the regression equation is the effect of competition from *P. keeni* on species *M. gapperi*, i.e., the competition coefficient α_{mp} (Crowell and Pimm 1976, Fox and Luo 1996). Similarly, the dependent variable for *P. keeni* was Y_{pj} (the standardized MNA of *P. keeni* at trap station j) and the standardized regression coefficient (b_m) of *M. gapperi*, as an independent variable in the regression equation is the effect of competition from *M. gapperi* on species *P. keeni*, (i.e., the competition coefficient α_{pm}). We then calculated contribution coefficients for each variable in the regression equation to determine how much that variable contributed to the variance in abundance of the dependent species. The contribution coefficient for each variable in the equation is the product of the standardized regression coefficient for the variable and the correlation coefficient between that independent variable and the dependent variable in the equation. The sum of all contribution coefficients in the equation equals the unadjusted coefficient of determination (R^2).

The unadjusted coefficient of determination can then be partitioned into $R^2_{\text{Competition}}$ the contribution coefficient attributable to interspecific competition (calculated from the local abundance of the other species) and R^2_{Habitat} the contribution coefficient attributable to habitat (calculated as the sum of the contribution coefficients of habitat variables in the equation), which must sum to R^2_{Total} the unadjusted coefficient of determination. We accepted $P \leq 0.05$ as an indication of statistical significance.

Results

MNA of voles and mice decreased from 1998 to 2000, but the patterns differed in the three habitats with breeding populations (Figure 1A–C). For habitat OG, both species showed a similar pattern of decrease from 1998 to 2000 (ratio of MNA voles to MNA Mice [V/M] is 1.30 then 1.56 then 2.00), with the number of voles always greater than the number of mice (Figure 1A). For habitat SG during the 1998 peak abundance period (Figure 1B), many more voles than mice were accommodated, but far fewer voles than mice in 1999 and more similar numbers in 2000 (V/M = 2.08:0.27:0.75). For habitat WO (Figure 1C), the number of voles was much greater than mice in 1998, but less in 1999 and then greater again in 2000 (V/M = 1.94:0.59:1.63). These changes in ratio with parallel decreases in voles and mice suggest a change in their interspecific relationships that may correspond to a shift in ecological dominance (see below).

We obtained additional insights by examining the percentage of trap stations occupied by each species (Figure 1D–F). For OG (Figure 1D), the ratio of the number of trap stations exclusively used by voles to those exclusively used by mice (Exclusivity Ratio = ER V/M) was 1.00 with identical percentages of stations occupied by each species at high abundance in 1998, but increasing dominance by voles (1.78) as MNA dropped in 1999, and even more so (2.19) with the lowest MNA in 2000, while the percentages of stations with both or neither species changed very little. In SG, voles dominated (exclusively using more microhabitats) at peak abundance, but this was reversed in 1999 and even more so in 2000 (ER V/M = 3.88:0.26:0.21), while the percentages of stations with both species showed even sharper decreases and those with neither showed marked increases (Figure 1E). For WO during peak abundance, voles again dominated, but to a lesser extent and this was reversed in 1999 with little further change in 2000 (ER V/M = 1.53:0.87:0.83), while the percentages of stations with both species showed very sharp decreases and those with neither showed very marked increases (Figure 1F), even more than that observed for SG (Figure 1E).

We conducted 12 stepwise multiple regressions to quantify effects of interspecific competition across four habitat types in temperate coastal rainforests: six regressions examined effects of voles versus habitat (14 independent variables) on mouse abundance during spring and autumn 1998–2000, and the other six examined the effects of mice versus habitat on vole abundance. These represented six sets of parallel interdependent regression models. With the exception of autumn 1998, all regressions yielded significant models with significant competition coefficients (Table 1). The intensity of competition (α) by mice on voles appeared to be similar to that of voles on mice (Table 1). Also, for both voles on

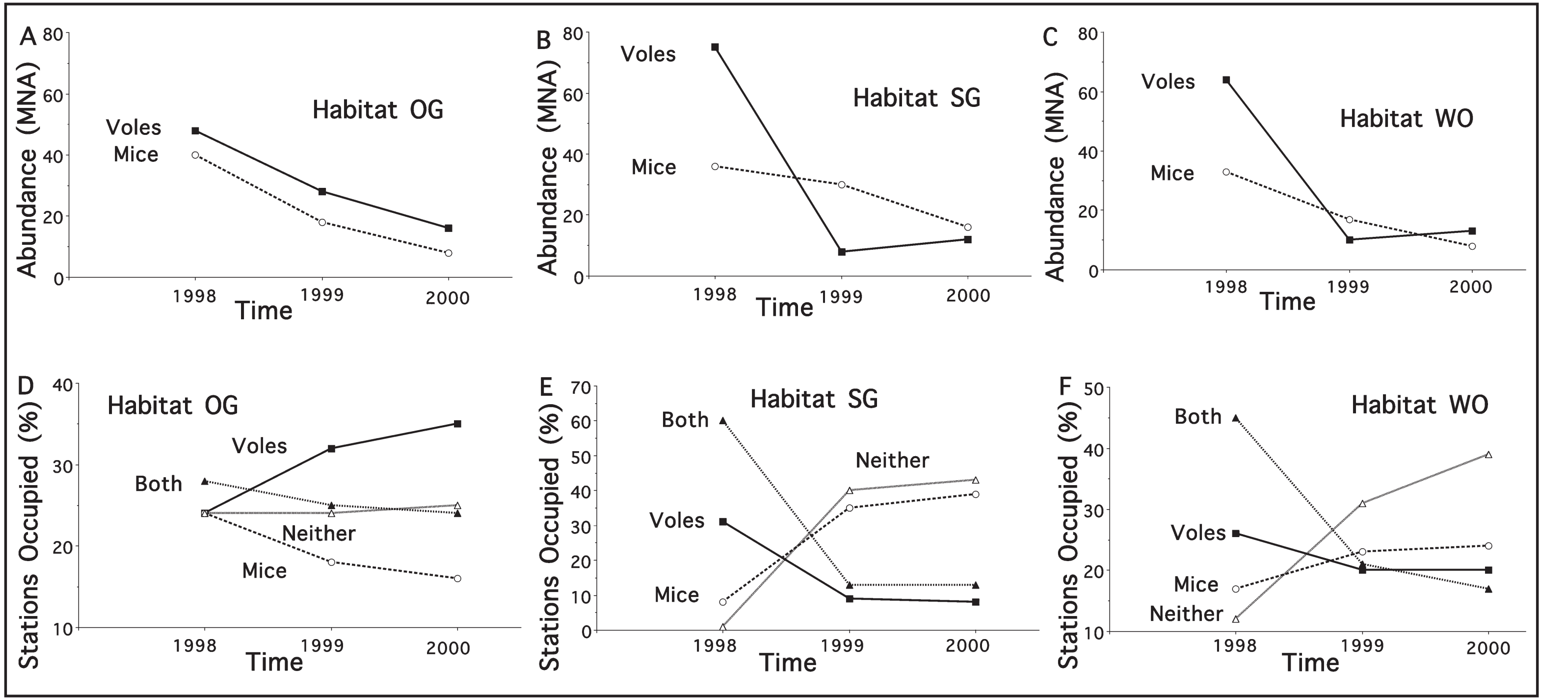

Figure 1. Minimum number of animals known to be alive (MNA) for red-backed vole (*Myodes gapperi*; solid lines and symbols) and Keen's mouse (*Peromyscus keeni*; dashed lines and open symbols) (from Smith and Nichols 2004) as a function of time during the study, 1998–2000, Wrangell Island, Alaska, shown separately for three habitats, together with the distribution of the percentage of trap stations occupied by each species exclusively, both species, and neither species as a function of time. MNA for Voles (solid squares) and Mice (open circles) in A) Habitat OG; B) Habitat SG; C) Habitat WO. Percent Stations Occupied for Voles (solid squares), Mice (open circles), Both species (solid triangles), and Neither species (open triangles) in D) Habitat OG; E) Habitat SG; F) Habitat WO.

TABLE 1. Competition coefficients (α) from stepwise multiple regression of standardized abundance data (Fox and Luo 1996) of red-backed voles (*Myodes gapperi*) and Keen's mouse (*Peromyscus keeni*) in temperate rainforests, Wrangell Island, Alaska. Abundance data are Minimum Number Alive (Krebs 1966) pooled across eight sites (two replicates x four habitat types), during 1998, 1999, and 2000. P_{reg} = probability of a significant model; P_{α} = significance of competition coefficient; $R^2_{\text{Competition}}$ is the contribution coefficient attributable to interspecific competition; R^2_{Habitat} is the contribution coefficient attributable to habitat variables; R^2_{Total} is the total contribution coefficient equal to the unadjusted coefficient of determination; R^2_{adj} is the coefficient of determination adjusted for number of variables in final regression model.

	1998		1999		2000	
Interspecific Effects	Spring (n = 127)	Autumn (n = 497)	Spring (n = 312)	Autumn (n = 113)	Spring (n = 187)	Autumn (n = 232)
Voles on mice						
α_{pm}	– 0.42	0	– 0.36	– 0.26	– 0.26	– 0.42
± S.E.	0.08		0.05	0.08	0.07	0.06
P_{reg}	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
P_{α}	< < 0.0001	> 0.25	< < 0.0001	< 0.0001	< 0.0001	< < 0.0001
$R2_{\text{Competition}}$	0.17	0.0000	0.13	0.08	0.07	0.18
$R2_{\text{Habitat}}$	0.02	0.02	0.08	0.22	0.11	0.05
$R2_{\text{Total}}$	0.19	0.02	0.21	0.30	0.18	0.23
$R2_{\text{adj}}$	0.17	0.02	0.20	0.27	0.16	0.22
Mice on voles						
α_{mp}	– 0.40	0	– 0.38	– 0.34	– 0.27	– 0.43
± S.E.	0.08		0.05	0.09	0.07	0.06
P_{reg}	< 0.0001	= 0.0068	< 0.0001	= 0.0012	< 0.0001	< 0.0001
P_{α}	< < 0.0001	> 0.50	< < 0.0001	< 0.0001	< 0.0001	< < 0.0001
$R2_{\text{Competition}}$	0.16	0.00	0.14	0.10	0.07	0.19
$R2_{\text{Habitat}}$	0.09	0.08	0.03	0.03	0.04	0.02
$R2_{\text{Total}}$	0.25	0.08	0.17	0.13	0.11	0.21
$R2_{\text{adj}}$	0.22	0.07	0.15	0.11	0.10	0.20

mice and mice on voles interspecific competition ($R^2_{\text{Competition}}$) appeared to explain more variation in the abundance of both species during spring 1998 and 1999 and autumn 2000 than did the variance associated with habitat (R^2_{Habitat}). This pattern was also true for the effect of mice on voles in autumn 1999; however, for voles on mice in autumn 1999 the variance explained by habitat appeared greater than that explained by interspecific competition. For both species, variation in abundance explained by interspecific competition was greatest during autumn 2000.

Multiple regression of standardized abundance and 14 independent variables within each habitat type yielded the similar pattern across habitats of more variation in vole or mouse abundance during spring 1998 and 1999 explained by interspecific competition and more variation in abundance during autumn 1998 and 1999 explained by habitat variables (Table 2). Although no significant differences could be demonstrated, for habitat OG the competition coefficient (α_{pm}) of voles on mice had a marginally greater value than that of mice on voles (α_{mp}) for all five trapping sessions in which competition coefficients could be determined. For habitat WO it was four of five and for MC it was two of three sessions; for habitat SG it was only one of four, although the one (spring 2000) was substantial. For both species, the largest competition coefficient (α) and the most variation in vole or mouse abundance explained by competition were recorded in MC during autumn 2000 (Table 2).

TABLE 2. Competition coefficients (α) from stepwise multiple regression of standardized abundance data (Fox and Luo 1996) of red-backed voles (*Myodes gapperi*) and Keen's mouse (*Peromyscus keeni*) for old-growth (OG), thinned second-growth (SG), wind-originated (WO) and mixed-conifer (MC) temperate rainforests, Wrangell Island, Alaska. Abundance data are Minimum Number Alive (Krebs 1966) pooled across two replicated sites in each of four habitat types, during 1998, 1999, and 2000 (Smith and Nichols 2004). The species with the numerically larger competition coefficient in each habitat in each trapping session is shown underlined. $R2_{Competition}$ is the contribution coefficient attributable to interspecific competition; $R2_{Habitat}$ is the contribution coefficient attributable to habitat variables; $R2_{Total}$ is the total contribution coefficient equal to the unadjusted coefficient of determination.

Year	1998		1999		2000	
Season	Spring	Autumn	Spring	Autumn	Spring	Autumn
Habitat (stations)						
Mouse Abundance			**Competition of Voles on Mice**			
OG (n)	(71)	(173)	(123)	(147)	(68)	(87)
α_{pm}	$\underline{-0.27}$	$\underline{-0.13}$	$\underline{-0.30}$	$\underline{-0.26}$	0.0	$\underline{-0.51}$
(± S.E.)	(± 0.12)	(± 0.10)	(± 0.09)	(± 0.08)		(± 0.09)
$R2_{Competition}$	0.07	0.01	0.09	0.07	0.0	0.26
$R2_{Habitat}$	0.05	0.11	0.03	0.07	0.17	0.04
$R2_{Total}$	0.12	0.12	0.12	0.14	0.17	0.30
Vole Abundance			**Competition of Mice on Voles**			
OG (*n*)	(71)	(173)	(123)	(147)	(68)	(87)
α_{mp}	– 0.26	– 0.10	– 0.28	– 0.25	0.0	– 0.50
(± S.E.)	(± 0.12)	(± 0.08)	(± 0.09)	(± 0.08)		(± 0.09)
$R2_{Competition}$	0.07	0.01	0.09	0.06	0.0	0.26
$R2_{Habitat}$	0.0	0.02	0.06	0.11	0.12	0.05
$R2_{Total}$	0.07	0.03	0.15	0.17	0.12	0.31
Mouse Abundance			**Competition of Voles on Mice**			
SG (*n*)		(175)	(75)	(79)	(50)	(65)
α_{pm}	N/A	0.0	– 0.21	– 0.22	$\underline{-0.46}$	– 0.25
(± S.E.)			(± 0.10)	(± 0.11)	(± 0.13)	(± 0.12)
$R2_{Competition}$		0.0	0.06	0.05	0.17	0.08
$R2_{Habitat}$		0.07	0.18	0.0	0.11	0.10
$R2_{Total}$		0.07	0.24	0.05	0.28	0.18
Vole Abundance			**Competition of Mice on Voles**			
SG (*n*)		(175)	(75)	(79)	(50)	(65)
α_{mp}	N/A	0.0	$\underline{-0.27}$	$\underline{-0.23}$	– 0.24	$\underline{-0.30}$
(± S.E.)			(± 0.11)	(± 0.11)	(± 0.13)	(± 0.12)
$R2_{Competition}$		0.0	0.07	0.05	0.09	0.09
$R2_{Habitat}$		0.09	0.04	0.04	0.29	0.0
$R2_{Total}$		0.09	0.11	0.09	0.38	0.09
Mouse Abundance			**Competition of Voles on Mice**			
WO (*n*)	(56)	(149)	(94)	(86)	(52)	(65)
α_{pm}	$\underline{-0.54}$	0.0	$\underline{-0.43}$	$\underline{-0.24}$	$\underline{-0.49}$	$\underline{-0.43}$
(± S.E.)	(± 0.12)		(± 0.10)	(± 0.10)	(± 0.11)	(± 0.11)
$R2_{Competition}$	0.31	0.0	0.19	0.07	0.23	0.18
$R2_{Habitat}$	0.09	0.10	0.02	0.13	0.21	0.10
$R2_{Total}$	0.40	0.10	0.21	0.20	0.44	0.28

TABLE 2 (*cont.*)

Year	1998		1999		2000	
Season	Spring	Autumn	Spring	Autumn	Spring	Autumn
Habitat (stations)						
Vole Abundance			**Competition of Mice on Voles**			
WO (*n*)	(56)	(149)	(94)	(86)	(52)	(65)
α_{mp}	-0.49	0.0	– 0.41	– 0.28	– 0.44	– 0.41
(± S.E.)	(± 0.11)		(± 0.09)	(± 0.10)	(± 0.12)	(± 0.11)
$R2_{Habitat}$	0.17	0.13	0.17	0.04	0.05	0.12
$R2_{Total}$	0.45	0.13	0.35	0.12	0.26	0.30
Mouse Abundance			**Competition of Voles on Mice**			
MC (*n*)			(21)	(27)	(17)	(15)
α_{pm}	N/A	N/A	0.0a	– 0.38	– 0.73	– 0.86
(± S.E.)				(± 0.17)	(± 0.19)	(± 0.13)
$R2_{Competition}$			0.0	0.19	0.48	0.70
$R2_{Habitat}$			0.0	0.28	0.06	0.12
$R2_{Total}$			0.0	0.47	0.54	0.82
Vole Abundance			**Competition of Mice on Voles**			
MC (*n*)			(21)	(27)	(17)	(15)
α_{mp}	N/A	N/A	0.0a	– 0.56	– 0.48	– 0.79
(± S.E.)				(± 0.17)	(± 0.16)	(± 0.20)
$R2_{Competition}$			0.0	0.28	0.31	0.64
$R2_{Habitat}$			0.39	0.04	0.40	0.10
$R2_{Total}$			0.39	0.32	0.71	0.74

Full information for MC and SG is lacking during spring 1998 and MC in autumn 1998 when no trapping occurred nor in MC during spring 1999 when no mice were captured.

Because of the patterns uncovered with stepwise multiple regression (Table 1 and Table 2), we used simple regression to examine variation in population density of each species over the 3-year study period (time) and variation in the intensity of interspecific competition relative to time and relative to the population density of each species for all trapping sessions, sessions during spring, and autumn sessions (Table 3). MC was excluded from this analysis because there were so few captures of mice (≤ 4) or voles (≤ 9) during each season.

Generally, vole and mouse abundance declined over the study (Figure 1) and density of both species explained significant variation in the intensity of interspecific competition of mice on voles, whereas only mouse density influenced the level of competition of voles on mice (Table 3). All regressions were significant during autumn; however, only vole and mouse abundance showed significant variation during spring, with time explaining 92% of the variation in vole MNA and 75% of the variation in mouse abundance (Figure 2). For interspecific competition, time also explained 87% of the variation in α_{pm} for voles on mice and 81% of the variation in α_{mp} for mice on voles during autumn (Figure 3). In addition, 76% of the variation in the intensity of mouse competition on voles (α_{mp}) was explained

TABLE 3. Summary of regressions of red-backed vole (*Myodes gapperi*) and Keen's mouse (*Peromyscus keeni*) density against time in years (1998–2000) and the effect of interspecific competition (α values from Tables 2 and 3) against time and population density of each species for all trapping sessions (both seasons and all years) and spring and autumn sessions 1998–2000, Wrangell Island, Alaska. (Bold typeface = statistical significance; - denotes inverse relationship)

Dependent variable	Independent variable	Probability	R^2
All trapping sessions			
Vole Density	**Time**	**0.01**	**– 0.35**
Mouse Density	**Time**	**< 0.01**	**– 0.46**
a (Mice on Voles)	Time	0.25	0.09
***a* (Mice on Voles)**	**Vole Density**	**0.01**	**– 0.34**
***a* (Mice on Voles)**	**Mouse Density**	**0.02**	**– 0.31**
a (Voles on Mice)	Time	0.38	0.05
a (Voles on Mice)	Vole Density	0.08	0.19
***a* (Voles on Mice)**	**Mouse Density**	**0.03**	**– 0.27**
Spring sessions			
Vole Density	**Time**	**< < 0.01**	**– 0.92**
Mouse Density	**Time**	**0.01**	**– 0.74**
a (Mice on Voles)	Time	0.32	0.17
a (Mice on Voles)	Vole Density	0.32	0.16
a (Mice on Voles)	Mouse Density	0.53	0.07
a (Voles on Mice)	Time	0.65	0.04
a (Voles on Mice)	Vole Density	0.53	0.07
a (Voles on Mice)	Mouse Density	0.76	0.02
Autumn sessions			
Vole Density	**Time**	**0.01**	**– 0.65**
Mouse Density	**Time**	**0.01**	**– 0.64**
***a* (Mice on Voles)**	**Time**	**< 0.01**	**0.81**
***a* (Mice on Voles)**	**Vole Density**	**< 0.01**	**– 0.71**
***a* (Mice on Voles)**	**Mouse Density**	**< 0.01**	**– 0.76**
***a* (Voles on Mice)**	**Time**	**< 0.01**	**0.87**
***a* (Voles on Mice)**	**Vole Density**	**0.01**	**– 0.62**
***a* (Voles on Mice)**	**Mouse Density**	**< 0.01**	**– 0.76**

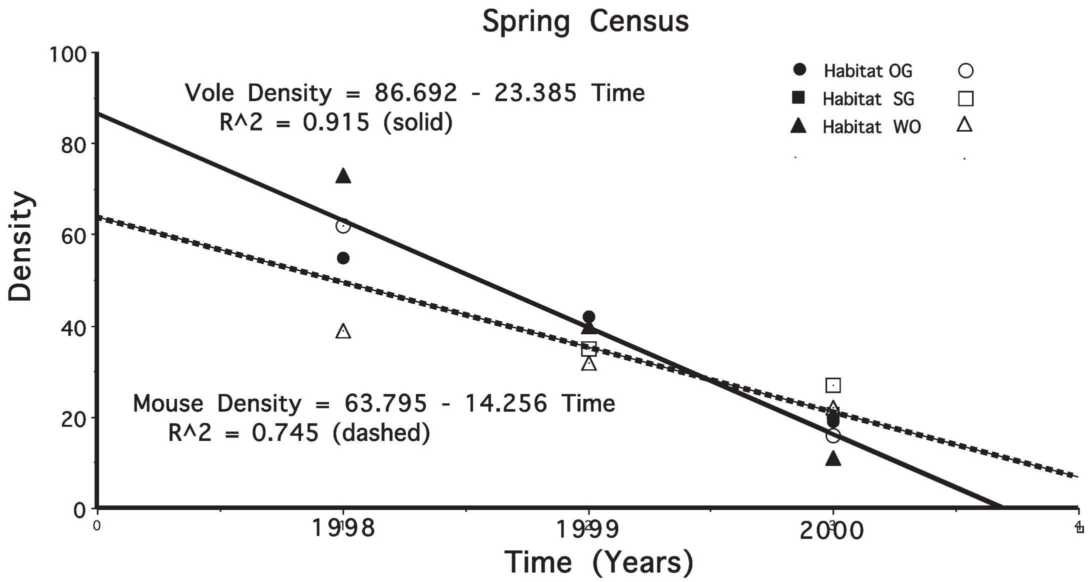

Figure 2. Linear regression relationships between red-backed vole (*Myodes gapperi*) density (solid lines and symbols) and Keen's mouse (*Peromyscus keeni*) density (dashed lines and open symbols) (Smith and Nichols 2004) as a function of time for the Spring Census during the study, 1998–2000, Wrangell Island, Alaska.

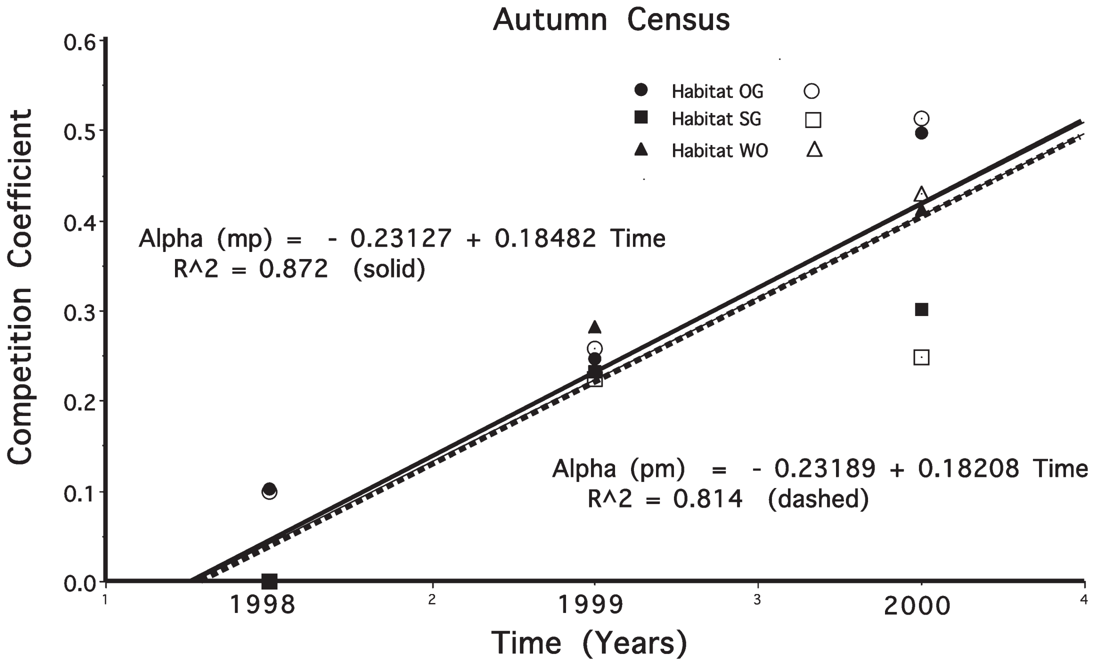

Figure 3. Linear regression relationship between intensity of interspecific competition (α_{mp}) of Keen's mouse (*Peromyscus keeni*) on red-backed vole (*Myodes gapperi*) (solid line and symbols) and α_{pm}, red-backed vole on Keen's mouse (dashed line and open symbols), as a function of time for the Autumn Census during the study, 1998–2000, Wrangell Island, Alaska.

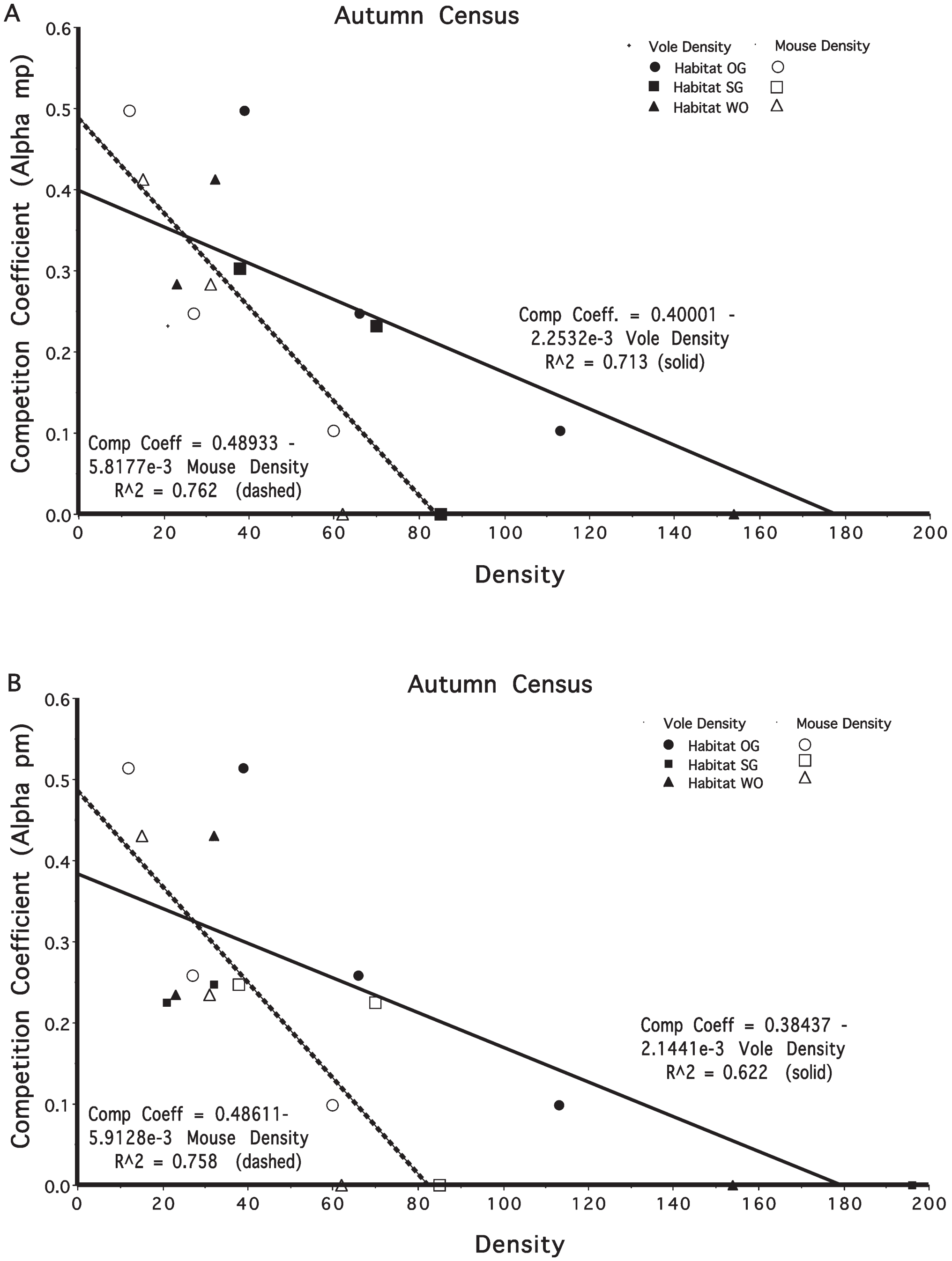

Figure 4. Linear regression relationship during the Autumn Census in four temperate rainforest habitats, 1998–2000, Wrangell Island, Alaska (Smith and Nichols 2004), between: A) the intensity of interspecific competition (α_{mp}) of Keen's mouse (*Peromyscus keeni*) on red-backed vole (*Myodes gapperi*) as a function of mouse density and as a function of vole density; B) the intensity of interspecific competition (αpm) of *Myodes gapperi* on *Peromyscus keeni* as a function of mouse density and as a function of vole density.

by changes in mouse density and 71% by changes in vole density during autumn (Figure 4A). Likewise, 76% of the variation in the intensity of vole competition on mice (α_{pm}) could be explained by mouse density and 62% could be explained by vole density (Figure 4B). These patterns were similar in all three habitats, with the possible exception of periods when vole densities were low in WO.

Discussion

Predictions and Patterns

The first of our four questions sought to quantify the contributions of habitat selection and interspecific competition in explaining the seasonal variation in abundance of voles and mice among habitat types. Because of the similarity in body size, we did not expect one species to necessarily dominate the second across all habitat types. Rather, in habitat types where both species flourish, we expected the intensity of interspecific competition to be greater for voles, the habitat specialist (Aubry et al. 1991, Nordyke and Buskirk 1991, Morris 1996, Sullivan et al. 2000, Smith et al. 2005). Voles are active throughout the day (Merritt 1981) and we expected that their continual presence and exploitation of resources in choice habitat would discourage intrusion by mice, which are nocturnal habitat generalists. Furthermore, because voles rely on mesic–wet forests (Getz 1968) with well-developed understories (Aubry et al. 1991, Nordyke and Buskirk 1991, Sullivan et al. 2000, Smith et al. 2005), we expected interspecific competition by voles would increase in intensity as habitat types become increasingly limited in microhabitats typical of OG, their primary habitat (Smith and Nichols 2004, Smith et al. 2005). Moreover, because the variation in fitness among habitats should be greater for specialists than generalists (Rosenzweig 1981) we expected habitat would play a much greater role in explaining variation in relative abundance of voles than interspecific competition from Keen's mouse. Accordingly, we expected variation in mouse abundance to mostly be explained by interspecific competition with voles, i.e., competitive coexistence through habitat selection (Rosenzweig 1981, Morris 1996).

Our findings do not support the prediction that habitat variables explain more significant variation in the abundance of voles than interspecific competition by mice (Table 1). The majority of variation in vole abundance across all four habitats was explained by interspecific competition from mice in all but one season (Autumn 1998). Furthermore, the competition coefficient of voles on mice (α_{pm}) was not consistently larger than mice on voles (α_{mp}); rather, α_{mp} and α_{pm} were similar in all census sessions. We observed one season (Spring 1998) in which the α of voles on mice was numerically larger than the α of mice on voles, and one season (Autumn 1999) in which α of mice on voles was larger than α of voles on mice, although neither were significantly different (Table 1). This finding was somewhat surprising given the apparent increase in ecological dominance of voles (i.e., number of exclusive microhabitats used) in OG and WO as global population density decreased in 1999 and 2000. Often body size determines the direction and outcome of interspecific competition between small mammals (Grant 1972, 1978). For example, the Australian swamp rat (*Rattus lutreolus*), a specialist, was consistently dominant in interspecific interactions with at least 50% smaller generalists in heathlands of Australia (*Pseudomys gracilicaudatus*; Thompson and Fox 1993) and Tasmania (*Pseudomys higginsi*; Luo et al. 1998). In southeastern Alaska, the body size of endemic *P. keeni* can vary significantly between island communities of the Alexander Archipelago (Hogan et al. 1993, Runck 2001). Further study of populations of both species on other islands likely would reveal whether body size affects the ecological interactions of southern red-backed voles and Keen's mouse.

The contribution of habitat variables versus interspecific competition in explaining vole and mouse abundance varied among habitat types (question 2), but only during periods with lower vole densities (Table 2). As expected, competition coefficients of voles (on mice) among natural habitat types (i.e., unmanaged forest) were smallest in OG and largest in MC, a habitat with numerous canopy openings and little understory vegetation (Smith et al. 2005). Average canopy cover in OG exceeds 80%, with large (> 74 cm diameter) trees and *Vaccinium* cover averaging 30 stems/ha and 20% cover, respectively. Average canopy cover of MC is < 50% with few, if any, large trees and less than half the *Vaccinium* cover of OG (Smith et al. 2005). Similarly, vole competition coefficients in SG were comparable to OG except when global vole and mouse densities across habitats were lowest (Spring 2000) and vole optimum habitat was most available. Elsewhere, voles rarely are captured in clearcuts or young, second-growth forests (Aubry et al. 1991, Nordyke and Buskirk 1991, Sullivan et al. 2000), probably because canopy removal desiccates the understory (Aubry et al. 1991, Nordyke and Buskirk 1991). Thinned second growth is new (1970s) to voles in southeastern Alaska and has very different structural attributes than natural habitat; it has a low, open canopy and few (if any) trees > 50 cm diameter, but *Vaccinium* cover can be similar to OG (Smith et al. 2005).

Regardless of season and year or habitat, the intensity of vole competition on mice (α_{pm}) did not appear to differ significantly (i.e., overlapping 90% confidence intervals) from that of mice on voles (α_{mp}). Furthermore, the contribution of interspecific competition in explaining variation in vole or mouse abundance did not appear to vary according to habitat or season and year (question 3). The one departure was in WO, where competition from mice explained the majority of variation in vole abundance in all but one season: when global vole and mouse populations were at their peak (Autumn 1998). The largest proportions of variation in vole habitat use contributed by competition from mice occurred during spring, especially when mouse and vole densities were at their lowest (2000). Although we expected interspecific competition to be more intense among breeding resident adults (Eccard et al. 2011), we did not expect competition from mice to explain more variation in vole abundance than habitat variables (Morris 1996), especially in WO. Older (> 100 yrs.) WO forests, which are dense-canopied second growth that regenerate following broad-scale catastrophic windstorms (Nowacki and Kramer 1998), typically are preferred by voles when population densities in OG approach carrying capacity (Smith and Nichols 2004).

For mice, the observed patterns were somewhat different from voles and more in agreement with our expectations (Table 2). Interspecific competition from voles explained a greater portion of the variation in mouse abundance across natural habitats during spring 1998 and 1999 (Table 2), when adult residents comprised a greater proportion of populations (Smith and Nichols 2004). During spring 2000, however, when population densities of both species were at their lowest, habitat variables, not interspecific competition with voles, explained more variation in mouse abundance in OG (question 4). This finding likely was a result of voles becoming more selective at lower densities (Morris 1996, Smith et al. 2005). That is, because voles were using less habitat space, mice had greater access to microhabitats in which the probability of encountering voles was considerably lower (Figure 1D).

Declines in global abundance over the study for both species were largely a result of fluctuations in spring population densities (Figure 1). Why voles and mice showed parallel declines in abundance over the study is unclear. Smith and Nichols (2004) speculated that a larger number of captures early in the study suggested ermine (*Mustela erminea*) likely had increased in response to very high vole populations and might have opportunistically preyed on Keen's mouse. If this were the case, then unique patterns we observed during the first year of the study might have in part been attributable to 'apparent competition' (Holt and Lawton 1993). Furthermore, population declines over the study undoubtedly resulted in decreased intraspecific competition, which we did not measure and which likely influenced the habitat use of both species, especially voles (Morris 1996). Interestingly, although the intensity of interspecific competition between mice and voles (both directions) at peak populations was greater during spring than autumn, declines in spring population density of both species apparently had little effect on their competition coefficients (Table 3). In contrast, autumn competition intensity was greatest when populations were at their lowest levels (2000). Moreover, competition coefficients of mice and voles increased with decreasing autumn populations of each species (Table 3), also suggesting that intensity of interspecific competition was greater during the season when juveniles comprised a larger proportion of the total population (Smith and Nichols 2004). Unfortunately, substantial variability and small effect sizes hindered our efforts to partition competitive interactions of juveniles and adults with stepwise regression.

Still, the inverse relationship between interspecific competition and population density in autumn is perplexing. Logically, one might expect increasing interspecific competition as the population densities of competing species increase. However, as conspecific density in optimum habitat increases beyond carrying capacity, individuals increasingly move into marginal habitats (Fretwell and Lucas 1970). Moreover, in our and similar studies (Morris 1996) habitat specialists became less specialized and behaved more like habitat generalists at high population densities. This was clearly demonstrated in our study by substantial changes in the percentage of available microhabitats used by voles, and to a much lesser degree, mice. At lower resident adult densities (spring, and during autumn with higher proportions of juveniles), voles are most specialized, presumably experience lower intraspecific competition for mesic forests (limited resource), encounter fewer mice in preferred microhabitats (i.e., lower percentage captures of both species at microhabitats in the same habitat type because each species occurs in preferred habitat types), and are exhibiting higher interspecific competition with mice where they are syntopic. A similar pattern occurred with mice; that is, at lower resident adult densities, mice presumably experience less intraspecific competition, encounter fewer voles in preferred microhabitats, and experienced higher competition with voles for mesic forest habitat where they co-occurred.

Thus, the pattern of greater interspecific competition at lower global population densities of both species could be explained by two autecological phenomena (possible apparent competition in 1998 excluded): density-dependent habitat selection, previously reported by Morris (1987b), Morris et al. (2000), and Lin and Batzli (2001), which manifested as a change in habitat type distribution and microhabitat selectivity of both voles and mice (reported also by Morris 1996) with changing global population densities of resident adults (most consistent intense interspecific competition during spring and at lower global densities in autumn when juveniles also comprised a larger proportion of autumn population); and changes in intraspecific competition, which also accompanied changes in global population densities of adults. How these ecological processes interacted to produce these patterns remains unclear because we did not measure intraspecific competition. Still, the ecological basis for our explanation is supported by the findings of several studies (Fretwell and Lucas 1970, Krebs 1966, Morris 1987b, Morris et al 2000).

Coexistence in Intact and Modified Landscapes

Habitat specialization can facilitate coexistence among competing species by making available underutilized habitat space for habitat generalists to exploit (Morris 1996). However, habitat affinities and the extent to which habitat specialization can facilitate coexistence will vary with environmental context (Morris 1989), especially composition and diversity of ecological communities. In rainforests of the Olympic Peninsula, for example, Keen's mouse flourishes in old-growth forests and is uncommon in early seral or fragmented forests in an ecological community with deer mice, *P. maniculatus* (Songer et al. 1997, Taylor 1999). Also, the role of interspecific competition versus habitat preference in determining habitat distribution of competing species can vary with population density (Vickery et al. 1987) and whether habitat selection is density dependent (Rosenzweig and Abramsky 1985, Morris 1987b, Morris et al. 2000). That is, during periods when population levels are low, resources become more available and more individuals are able to occupy optimal habitat. However, as population density increases, resources become depleted, intraspecific competition intensifies, and animals move into suboptimal habitat because expected fitness in optimal habitat diminishes as populations approach carrying capacity (Fretwell and Lucas 1970). Thus, marginal habitats are occupied during periods when population density and intraspecific competition are greatest, whereas optimum habitats support the largest fraction of the population when densities are lowest (Fretwell and Lucas 1970, Morris 1996).

On Wrangell Island, the southern red-backed vole and Keen's mouse are the only two terrestrial rodents in rainforest communities. With relatively few competitors and a diversity of habitat types and resources, it is reasonable to expect that microhabitat selection will play a significant role in the coexistence of voles and mice (Miller 1964, Rosenzweig and Winakur 1969, Hallett 1982, Rosenzweig 1989, Morris 1996, Bonesi and Macdonald 2004). During the initial study of habitat relations, both species exhibited density-dependent habitat selection, although the variation reported for Keen's mouse was only a fraction of that of red-backed voles (Smith et al. 2005). Over the period of their study, vole populations declined precipitously such that in 2000 the population was about 20% of the global population in 1998 and the relative abundance of voles in OG increased by about 350%. During that same period, we observed that the percentage of available trap stations where voles were exclusively captured increased from 27% to 36% in OG and decreased from 28% to 12% in WO, MC, and SG. Also, we noted that the percentage of trap stations where voles were not captured increased from 6% to 73%, all of which confirming OG as optimum habitat and that individuals became increasingly selective in all habitat types as population density declined. Indeed, Smith et al. (2005) reported only one significant habitat model at peak densities, whereas at much lower vole densities they reported significant models across all habitat types and during both seasons. Furthermore, body mass, juvenile survival, and the percentage of female voles that were reproductive were higher in old-growth forests than SG (Smith and Nichols 2004).

A similar pattern occurred with mice but in SG; relative abundance increased by 30% as the global population decreased by 70% over the study (Smith et al. 2005). In our study, percentage of trap stations with exclusive captures of mice increased from 8% to 41% in SG, but changed little (21% to 20%) in other habitat types during that same period. SG is apparently the optimum habitat of Keen's mouse in southeastern Alaska; population density, summer survival rates, and percentage of reproductive females were consistently higher and annual fluctuations in autumn populations were much smaller than in the other habitat types (Smith and Nichols 2004). Similar conclusions were reported for Keen's mouse populations on a nearby island without red-backed vole populations (Hanley and Barnard 1999).

Thus, at low population densities the two species appear to coexist in a habitat mosaic largely through differential habitat selection; voles disproportionally occur in OG, whereas mice favor SG, but with a more uniform distribution among habitat types than voles (Smith and Nichols 2004). A similar pattern occurred in montane coniferous forests, where voles preferred mesic forests at all densities but occurred almost exclusively in mesic forests at very low densities, whereas *P. maniculatus* selected xeric habitats (Morris 1996). Throughout much of its range, the southern red-backed vole has been characterized as a specialist of late-seral forest habitat (Lovejoy 1975, Ramirez and Hornocker 1981, Scrivner and Smith 1984, Keinath and Hayward 2003), unable to establish breeding populations in recent clearcut or young-growth coniferous forests (Aubry et al. 1991, Sullivan et al. 2000). Much less is known about Keen's mouse (Smith et al. 2001), but previous studies in southeast Alaska clearly demonstrated that populations flourish in a wide range of habitats and suggest its optimum habitat is early seral forest (Van Horne 1981, Hanley and Barnard 1999).

Voles may be unable to persist in clearcut or young growth coniferous forests of western North America because of high physiological requirements for water (Getz 1968, Orrock et al. 2000) and because of dramatic vegetative and microclimatic changes in the understory that typically accompany canopy removal. In southeastern Alaska, voles were captured in SG throughout the study (Smith and Nichols 2004), although the fraction of the global population in SG at low densities was small (Smith et al. 2005). Perhaps a cooler, wetter climate in southeastern Alaska mitigates desiccation following canopy removal and renders open-canopied SG more suitable for voles. Still, vole use of microhabitats in recently logged rainforests was male-biased and approached being random, and the expected fitness of individuals was lower than in old-growth forests (Smith et al. 2005).

Evidence from this study and Smith et al. (2005) demonstrated that when voles move into marginal habitats they were less selective and used much of the available habitat space almost indiscriminately. Consequently, voles presumably encountered Keen's mouse more often (45% of trap stations) than when both species were at their lowest densities (15%) and voles were mostly in OG while mice were mostly in SG. Still, the most intense competition in both directions occurred in MC during 1999 and 2000. The evidence from our study is limited; however, we suggest this occurred because, despite being generally poor habitat overall, some microhabitats in MC represent relatively high quality habitat for both species. MC habitat is heterogeneous at the scale of a few meters (Smith et al. 2005), with patches of rainforests similar to OG in structure and composition interspersed within expanses of peatlands of treeless muskegs and scrub forests. Of the three suboptimal habitats, features of those patches are most similar to OG and thus attractive to voles (Smith et al. 2005). Because relatively few voles occur in MC at lower densities it presumably is also attractive to Keen's mouse.

Obviously, there are factors not explicitly considered in our study that can influence habitat selection and interspecific competition, not the least of which are intraspecific competition (Fretwell and Lucas 1970) and predation (Morris 1996). It is suffice to say that both density-dependent habitat selection and interspecific competition facilitate coexistence of populations of voles and mice on Wrangell Island. More detailed study is clearly needed to further elucidate how season, population density, body size, intraspecific competition, and other interspecific interactions, such as predation, may influence their coexistence on other islands and across mainland southeastern Alaska.

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