

Correlates of microhabitat use and density of *Clethrionomys gapperi* and *Peromyscus keeni* in temperate rain forests of Southeast Alaska^{*}

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Abstract We studied red-backed vole *Clethrionomys gapperi* and Keen's mouse *Peromyscus keeni* populations in the Alexander Archipelago to test predictions regarding habitat relations in temperate rain forest of southeastern Alaska during August–September 1998 and 2000 and April–May 1999 and 2000. We measured 26 vegetative and structural features to correlate abundance among and microhabitat use within gap-phase old growth, multi-cohort old growth, pre-commercially thinned young (23-yr-old) growth, and peatland mixed-conifer forests. Populations of both species were higher in 1998 than 1999 and 2000. Both species used microhabitats randomly in 1998, but were highly selective in 1999–2000. Correlates of microhabitat use varied between seasons and among habitats, but *C. gapperi* captures were most often positively correlated with the percent cover of deciduous shrubs in the understory. Microhabitats used by *P. keeni* had less moss cover on the forest floor, but in gap-phase were directly related to the probability of capturing a *C. gapperi*. Density of both species during both seasons was directly correlated with decayed downed wood in the understory. Density of *P. keeni* in spring explained 62% of the variation in *C. gapperi* density, which in turn explained 89% of the variation in *P. keeni* density. Our results corroborate the findings of earlier studies that *P. keeni* in southeastern Alaska flourishes in a variety of habitats, especially early seral forests; but, departed from the general conclusion that *C. gapperi* populations in western landscapes achieve their highest densities in late-seral coniferous forests. Unlike populations elsewhere in north-western North America, *C. gapperi* may be able to persist in rain forest patches where the overstory has been removed. Peatland mixed-conifer forest contributed little to breeding populations of *C. gapperi* or *P. keeni* and thus is unlikely to mitigate any impacts of broad-scale clearcut logging of productive old-growth rainforests [Acta Zoologica Sinica 51 (6): 973–988, 2005].

Key words Alexander Archipelago, *Clethrionomys gapperi*, Density, Ecological correlates, Habitat distribution, Microhabitat use, *Peromyscus keeni*, Population ecology, Southeast Alaska, Temperate rain forest, Wrangell Island

阿拉斯加东南部温带雨林加氏 和肯氏鹿鼠密度与微生境利用的相关性^{*}

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摘要 为了验证对阿拉斯加东南部温带雨林中有关栖息地关系的预测, 我们于 1999 年和 2000 年 8–9 月以及 1999 年和 2000 年 4–5 月研究了亚历山大群岛加氏 (*Clethrionomys gapperi*) 和肯氏鹿鼠 (*Peromyscus keeni*) 种群。我们测量了 26 个植被和结构特征以检验林隙老龄生长林、多时代老龄生长林、采伐前壮龄 (23 岁) 生长

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林和泥炭混交针叶林的丰富度与微栖息地利用的相关性。微栖息地利用随季节和栖息地而变化,但加氏与林下落叶灌木覆盖度的正相关最显著。肯氏鹿鼠利用的微环境的林地有较少的苔藓,但是林隙与抓获加氏的概率有直接关系。两种鼠在两个季节的密度与林下腐朽的倒木直接相关。春季的肯氏鹿鼠密度说明加氏密度变化的62%,说明肯氏鹿鼠密度变化的89%。我们的结果印证了早期对阿拉斯加东南部肯氏鹿鼠在各种栖息地尤其早期的演替林中兴旺时的研究;但偏离了西部地貌中肯氏鹿鼠种群在晚期演替针叶林中达到最高密度的普遍结论。与北美西北部其它地区的种群不同,加氏能持久生活在上层被砍伐的雨林板块中。泥炭针叶混交林对两种鼠的繁殖种群几乎没有贡献,因而不可能减轻对多产的老龄生长雨林大规模皆伐所造成的影响[动物学报 51(6): 973-988, 2005]。

关键词 阿拉斯加群岛 加氏 密度 生态相关性 栖息地分布 微栖息地利用 肯氏鹿鼠 阿拉斯加东南部 温带雨林 兰格尔岛

Despite the ecological importance of small mammals to temperate forest communities (Maser et al., 1978; Li et al., 1986; Elkinton et al., 1996; Cazes et al., 1999; Moore 1999; Sullivan et al., 1999; Terwilliger and Pastor, 1999; Sirotiak and Huntley, 2000), the mammalian fauna of Southeast Alaska has been poorly studied (MacDonald and Cook, 1996; Smith et al., 2001). Two common small mammals of coastal temperate rain forest are the red-backed vole *Clethrionomys gapperi* and Keen's mouse *Peromyscus keeni* (MacDonald and Cook, 1996; Smith et al., 2001; Smith and Nichols, 2004). *C. gapperi* ranges across much of northern North America (Hall, 1981) and is common in mesic forest habitats in the Hudsonian and Canadian life zones (Merritt, 1981). In Southeast Alaska, *C. gapperi* is known from the narrow mainland and nearshore islands south of the Stikine River*, where it occurs as four endemic subspecies (MacDonald and Cook, 1996). *P. keeni* is a sibling species of the more ubiquitous *P. maniculatus*, with three island endemic subspecies and two subspecies with ranges that are largely restricted to Southeast Alaska (Hogan et al., 1993; MacDonald and Cook, 1996). *P. keeni* occurs across the Alexander Archipelago and on the mainland portion of Southeast Alaska east and south of Glacier Bay (MacDonald and Cook, 1996), where it inhabits riparian and upland old-growth forests (Hanley and Barnard, 1999; Smith and Nichols, 2004), fens (Smith et al., 2001), and regenerating second-growth forests (Van Horne, 1981; Smith and Nichols, 2004).

Little is known about the natural history, demography, or habitat relations of *C. gapperi* in Southeast Alaska (Smith et al., 2001; Smith and Nichols, 2004). The optimal habitat for *C. gapperi* in western North America is reputedly mature, mesic coniferous forests (Merritt, 1981; Jerry, 1984; Nordyke and Buskirk, 1988; Aubry et al., 1991; Sullivan et al., 1999, 2000; but see Taylor, 1999;

Ramirez and Hornocker, 1981; Scrivner and Smith, 1984; Raphael, 1988; Pearson and Ruggiero, 2001). In western coniferous forests, *C. gapperi* populations show acute sensitivity to canopy removal (Scrivner and Smith, 1984; Aubry et al., 1991; Sullivan et al., 1999, 2000; Keinath and Hayward, 2003) and habitat fragmentation (Bayne and Hobson, 1998; Bowman et al., 2001a; Mech and Hallett, 2001); population response to overstory removal varies depending upon size and distribution of canopy gaps (Hayward et al., 1999). In addition to a dense overstory, *C. gapperi* prefers mesic stands with abundant coarse woody debris (CWD) and vegetative cover in the understory (Wywiałowski and Smith, 1988; Nordyke and Buskirk, 1991; Bowman et al., 2001a; Keinath and Hayward, 2003; Ucitel et al., 2003; Hadley and Wilson, 2004).

In contrast, *P. keeni* seems to flourish in a variety of habitats (Hanley and Barnard, 1999; Smith et al., 2001), including a broad range of forest seral stages (Van Horne, 1982a; Hanley, 1996; Taylor, 1999; Smith and Nichols, 2004). However, information regarding its response to habitat disturbance, particularly population responses to clearcut logging, has been limited and varied. Hanley (1996) reported similar densities of *P. keeni* between old growth and even-aged, second growth in Southeast Alaska. On the Olympic Peninsula, *P. keeni* was clearly more abundant in old growth (Songer et al., 1997; Taylor, 1999) than in younger seral stages. The highest population densities occurred in continuous forests, with significantly lower densities in fragmented landscapes (Songer et al., 1997). Little is known about the fine-scale distribution or abundance of *P. keeni* relative to microhabitat features.

Knowledge of population ecology is fundamental to understanding and projecting the response of indigenous vertebrates to habitat modification (Morris, 2003; Van Horne, 1981). Furthermore, restoration

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of managed landscapes to sustain viable populations of old-growth associated endemics requires a thorough understanding of habitat requirements (Smith et al., 2004). The purpose of this paper is to quantify the habitat relations of *C. gapperi* (hereafter voles) and *P. keeni* (hereafter mice) among four habitats in Southeast Alaska. Specific objectives were to test the following predictions: 1) voles achieve their highest densities in late-seral forest; 2) voles avoid forests without an overstory; 3) vole abundance is correlated with shrub cover and coarse woody debris in the understory; 4) mice flourish in a wide range of forest habitats; and 5) mice achieve their highest densities in early seral forest.

1 Materials and methods

1.1 Study area

The study was conducted on Wrangell Island (56°30'N, 132°17'W), a nearshore island of ~500 km² with elevation ranging from sea level to 853 m (Smith and Nichols, 2004). Across the region, temperate coniferous rain forest dominates the landscape from shoreline to ca. 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 peatlands) or riparian (Harris and Farr, 1974). About 50% of Wrangell Island was productive forestland, of which about 11% was clearcut-logged during the last 4 decades. The two old-growth habitats were stands with contrasting disturbance regimes and notable differences in forest canopy, understory, and stand structure (Nowacki and Kramer, 1998). Gap-phase old growth usually occurs on northerly slopes (sheltered from prevailing windstorms) and experience frequent, less intense disturbance that results in blow-downs of 1 to a few trees. This habitat is relatively homogeneous at the scale of forest patches with fine scale spatial heterogeneity resulting from canopy gaps; trees are typically >400 years old. In contrast, multi-cohort old growth typically has a southerly exposure and experiences infrequent (100–200 years), catastrophic disturbance from windstorms that usually blow down 10–100 ha of forest (Nowacki and Kramer, 1998; Kramer et al., 2001). This habitat is spatially heterogeneous at the habitat scale with patches of uniform diameter trees (typically 100–200 years old) distributed within the stand; trees are rarely >300 years old.

The overstory of old-growth forests 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 (>75 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 (Hanley and Brady, 1997; Ver Hoef et al., 1988). Because of a more uniformly dense canopy, multi-cohort forest usually has sparser understory vegetation than gap-phase. In contrast, peatland mixed-conifer sites are typified by poor drainage and shallow and organic soils with patches of more productive mixed-conifer forests that occur on elevated sites of deeper mineral soils. Conifer vegetation ranges 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 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 (Pawuk and Kissinger, 1989).

1.2 Habitat use

We live-trapped 6 (2 replicates each of gap-phase, multi-cohort, and peatland mixed-conifer habitats) 1-ha (100 m × 100 m) grids in largely unmanaged landscapes and two 1-ha grids in thinned young-growth stands in an intensively logged (47% of old growth converted to early seral forests) watershed. Both logged sites were 23-yr-old second-growth forest thinned to 5.5 m (± 25%) spacing during spring 1998. Individual study sites were replicates of 4 habitats selected according to type and frequency of disturbance, overstory cover, and management history: 1) gap-phase old growth; 2) multi-cohort old growth; 3) peatland mixed-conifer; and 4) thinned young (25 yr-old) growth. Replicates were located in the same watershed to minimize geographical variation, but >800 m apart to achieve independence. All grids were an 11 × 11 array of trap stations at 10-m intervals. Smith and Nichols (2004) estimated population density based on a Lincoln-Petersen model and effective area sampled as determined with assessment lines (Swift and Steinhorst, 1976; Van Horne, 1982b). Trapping, handling, and marking of study animals followed Smith and Nichols (2004) and adhered to guidelines of the American Society of Mammalogists (ASM Animal Care and Use Committee, 1998).

1.3 Habitat variables and sampling

We measured 26 vegetative and structural habitat elements using two nested plots (Spies et al., 1988; Rosenberg and Anthony, 1992; Carey, 1995) at trap stations where voles or mice were captured and at every third trap station without a capture. Habitat

elements included understory vegetation, dead (i. e., snags) and live standing trees, and volume and decay class of downed woody material (Table 1). Understory habitat variables were visually estimated (percent cover) in 1×1 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 (9 subplots/station). Within each subplot, we estimated percent cover (to the nearest 5%) of herbaceous vegetation, moss, woody debris (<25 cm in diameter), and water. We also recorded percent cover of three groups of woody vegetation within each of two vertical strata: < 30 cm and 30 – 150 cm. The three

groups were: 1) *Vaccinium*, of which the most common species were red huckleberry *Vaccinium parvifolium* and two species of blueberry *V. alaskaense* and *V. ovalifolium*; 2) all other deciduous species; and 3) conifer species, which were 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 Southeast Alaska (Hanley and Brady, 1997). The mean values of the nine subplots were used to describe the understory at each trap station.

Table 1 Habitat features measured within study grids where trap stations were centers of a 20-m circular plot in gap-phase and multi-cohort old-growth western hemlock *Tsuga heterophylla*-Sitka spruce *Picea sitchensis* forests, thinned young-growth (23 yr old), and peatland-scrub/mixed-conifer forests, Wrangell Island, Southeast Alaska during 1999 – 2000

Habitat variable	Description
Vacc 1	Mean percent cover of <i>Vaccinium</i> ≤ 0.3 m tall.
Vacc 4.5	Mean percent cover of <i>Vaccinium</i> between 0.3 m and 1.5 m in height.
Decid 1	Mean percent cover of deciduous shrubs (except <i>Vaccinium</i>) ≤ 0.3 m tall.
Decid 4.5	Mean percent cover of deciduous shrubs (except <i>Vaccinium</i>) between 0.3 m and 1.5 m in height.
Conifer 1	Mean percent cover of conifer seedlings ≤ 0.3 m tall.
Conifer 4.5	Mean percent cover of conifer saplings between 0.3 m and 1.5 m in height.
Moss	Mean percent cover of moss.
Herb	Mean percent cover of herbaceous vegetation ≤ 1.5 m.
Wood	Mean percent cover of downed wood ≥ 1 m long and <25 cm diameter at the midpoint diameter.
Water	Mean percent cover of surface water.
Decay I	Volume (m^3)/ m^2 of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a I.
Decay II	Volume (m^3)/ m^2 of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a II.
Decay III	Volume (m^3)/ m^2 of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a III.
Decay IV	Volume (m^3)/ m^2 of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a IV.
Decay V	Volume (m^3)/ m^2 of downed wood ≥ 10 cm midpoint diameter and ≥ 1 m long in decay class ^a V.
Stump	Density of stumps ^b .
Tree 74	Density of trees >1.5 m tall and with dbh >74 cm.
Tree 50 – 74	Density of trees >1.5 m tall with dbh between 50 and 74 cm.
Tree 10 – 49	Density of trees >1.5 m tall with dbh between 10+ and 49 cm.
Tree 5 – 10	Density of trees >1.5 m tall with dbh between 5 and 10 cm.
Soft snag 74	Density of snags ^c >1.5 m tall and >74 cm dbh with <2% of limbs ≥ 30 cm remaining.
Soft snag 50 – 74	Density of snags ^c >1.5 m tall and between 50 and 74 cm with <2% of limbs ≥ 30 cm remaining.
Soft snag 10 – 49	Density of snags ^c >1.5 m tall and between 10+ and 49 cm with <2% of limbs ≥ 30 cm remaining.
Hard snag 74	Density of snags ^c >1.5 m tall and >74 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining.
Hard snag 50 – 74	Density of snags ^c >1.5 m tall and between 50 and 70 cm with $\geq 2\%$ of limbs ≥ 30 cm remaining.
Hard snag 10 – 49	Density of snags ^c >1.5 m tall and between 10+ and 49 cm dbh with $\geq 2\%$ of limbs ≥ 30 cm remaining.

a: Decay classes according to Fogel and others (1973), as modified by Sollins (1982). b: Base of a topped off dead tree that is between 0.3 – 1.5 m tall. c: Standing dead tree >1.5 m tall.

We also quantified density (based on either 12.6 or 20-m radius circular plots) of live trees and snags (all species pooled). 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, we recorded 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. Within a 20 m radius, we recorded number of live trees and snags in each of two classes of larger trees: 50–73 cm, and ≥ 74 cm (Table 1). Similarly, volume of downed wood, segregated by decay class (Fogel et al., 1973), was estimated in either 12.6 m or 20 m radius of the trap station. For each piece of downed wood, the following information was collected: midpoint diameter (cm), decay class (I–V), and length; length and circumference were used to calculate volume. Decay status was determined for downed woody material > 10 cm in midpoint diameter using the scheme modified by Sollins (1982) cm, and ≥ 74 cm (Table 1). Similarly, volume of downed wood, 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 within the context of the forest floor (e.g., above forest floor, slightly covered with moss, or indistinguishable from forest floor). All pieces of downed wood 25–50 cm (midpoint diameter) were counted within a 12.6 m radius plot, whereas all larger pieces (> 50 cm) were counted in a 20 m radius plot. Amount of downed wood for each trapping station was estimated as volume (m^3) per m^2 for each decay class.

1.4 Statistical analysis

We used a combination of descriptive statistics and explanatory models to relate microhabitat and forest patch conditions to microsite use and density of voles or mice in each habitat. Within microhabitats, we examined the relationship between the likelihood of capturing a species and habitat characteristics and the likelihood of capturing the second species among 800 trap stations (eight 10×10 grids, i.e., 2 replicates of each habitat). The likelihood of capturing voles or mice at a trap station was computed as total number of captures divided by total number of trap nights corrected for closed or malfunctioning traps (Nelson and Clark, 1973). Before analyzing micro-

habitat use, we used histograms to examine the frequency distribution of captures for each habitat and season. Also, to discover if likelihood of capture was influenced by an ‘edge effect’, i.e., trap stations on the grid perimeter had greater probability of capturing animals than ‘interior’ trap stations (Carey et al., 1999), we used simple linear regression (SAS, 2000) to investigate captures relative to the distance of concentric trap lines ($n = 5$) from the grid perimeter. We used ANOVA to compare microhabitat characteristics among concentric lines of trap stations ($n = 5$) to determine if an edge effect would bias our habitat analyses. We pooled capture data across 1999–2000 to improve precision in habitat modeling, but we analyzed data from autumn 1998 separately because populations of voles and mice were significantly higher during 1998 than in subsequent years (Smith and Nichols, 2004).

To model habitat selection, trap stations were categorized as either capturing each species (realized habitat) or not (unrealized habitat; Carey et al., 1999). We did this because of anticipated problems with model convergence (Stokes et al., 1995) using a polytomous response (no captures versus one capture versus > 1 capture) when likelihood of capture is greatly skewed toward one response level (e.g., 0 captures; Smith et al., 2004), and because we had little ecological justification for delineating distinct categories for multiple captures, especially differentiating between sites with one versus two captures.

For each of the 26 variables and vole and mouse captures, we used summary statistics, box and whisker plots, and histograms to examine distribution and variance structure. All measurements recorded as percent cover were arc sine transformed prior to analysis (Zar, 1999). Also, we used factor analysis to generate multivariate habitat factors (Carey et al., 1999). Factor analysis uses predictive data (26 habitat variables in our study) and creates ‘factors’ using correlation matrices; the first factor accounts for a portion of the variance in the original variables, whereas the second is created based on the highest correlation to the original variables after accounting for variation explained by the first factor, and so on. We used VARIMAX rotation within PROC FACTOR (SAS, 2000) to rotate factors to obtain new orthogonal (uncorrelated) variables, and visual inspection of ‘scree plots’ to identify factors used in subsequent modeling efforts (Cody and Smith, 1997: 257). Factor loadings (correlation of each factor with the 26 habitat variables) were used to interpret orthogonal habitat factors. We used coefficients from a correlation matrix of all habitat variables to determine extent to which habitat variables were potentially redundant in explaining variation in the response vari-

able. This information was used to develop models through an evaluation of variable selection in stepwise logistic regression (SLR) and an interpretation of factor loadings following factor analysis.

We used SLR to examine relationships between captures of a species (0 vs. ≥ 1 captures) in each habitat and season and the likelihood of capturing the second species and microhabitat characteristics according to measured variables (8 models) or multivariate habitat factors (8 models). Measured variables or habitat factors were entered into a model if the $P \leq 0.25$, but were retained only if $P \leq 0.05$. We repeated logistic regression analysis using the best subsets selection procedure (Cody and Smith, 1997) and obtained similar results. For each significant variable or factor in the final logistic regression models, we calculated confidence intervals on the odds-ratios, which were based on the profile likelihood (SAS, 2000; Smith et al., 2004). Thus, parameter estimates are interpreted as the odds of capturing a vole or mouse given a one-unit increase in the habitat parameter (e. g., density of trees per ha) after being adjusted for the effects of other habitat elements in the model. We used the Hosmer and Lemeshow test to evaluate the suitability of each model, and examined several measures of goodness-of-fit to evaluate the association of predicted captures and observed responses (SAS, 2000). We generated classification tables within PROC LOGISTIC to evaluate the performance of models in predicting 'used' versus 'unused' microsites.

2 Results

2.1 Vole and mouse distributions among habitats

During September 1998 and spring (April – May) and autumn (August – September) 1999 – 2000, we caught 682 and 540 individual voles and mice, respectively. Autumn populations of both species were markedly higher in 1998 than in 1999 or 2000, but with different consequences for habitat use. The ranking of habitats (based on density) remained unchanged throughout the study for mice, but not for voles. Mean densities ($\pm SE$) in 1998 were highest in young growth for voles ($25.5 \pm 5.0/\text{ha}$) and mice ($7.9 \pm 0.6/\text{ha}$), whereas gap-phase had the lowest densities of voles ($9.6 \pm 0.9/\text{ha}$) and mice ($5.6 \pm 1.2/\text{ha}$). Peatland mixed-conifer was not sampled in 1998, but had the lowest density of voles and mice during spring ($1.2 \pm 0.2/\text{ha}$ and $0.2 \pm 0.2/\text{ha}$, respectively) and autumn ($0.7 \pm 0.4/\text{ha}$ and $0.4 \pm 0.4/\text{ha}$, respectively) 1999 – 2000. During autumn 1999 – 2000, vole densities were higher in gap-phase old growth than young growth, which was ranked lower but had similar vole densities as multi-cohort old growth. Corresponding vole densities in

gap-phase, multi-cohort, and young-growth were $2.6/\text{ha}$ (± 0.8), $3.2/\text{ha}$ (± 0.6), and $3.6/\text{ha}$ (± 1.4) during spring, and $4.5/\text{ha}$ (± 0.5), $3.4/\text{ha}$ (± 0.4), and $3.4/\text{ha}$ (± 1.2) during autumn. Mean densities of mice in gap-phase, multi-cohort, and young growth during spring were $2.4/\text{ha}$ (± 0.4), $2.5/\text{ha}$ (± 0.6), and $2.8/\text{ha}$ (± 0.9), respectively, whereas corresponding autumn densities were $1.8/\text{ha}$ (± 0.2), $2.2/\text{ha}$ (± 1.0), and $5.0/\text{ha}$ (± 1.4).

2.2 Microhabitat use

Distributions of captures per trap station among microhabitats were skewed toward zero for all habitats especially in 1999 and 2000 for voles ($\bar{X} = 68\%$, range 42% – 87%) or mice ($\bar{X} = 67\%$, range 50% – 98%). Captures per trap station among microhabitats ranged 1 – 10, of which 26% had single captures, 8% had two captures, and 7% had ≥ 3 captures. In 1998, the percentage of stations without a capture was lower than subsequent years for voles ($\bar{X} = 28\%$, range 9% – 47%) and mice ($\bar{X} = 39\%$, range 33% – 48%). With few exceptions, the capture rate of voles and mice was unrelated to proximity of stations to the grid perimeter in all habitats during both seasons ($r^2 = 0.00 - 0.80$, $P = 0.82 - 0.03$). The few instances of capture rates decreasing from the perimeter toward the grid interior, were significant only for mice in gap-phase during spring 1999 – 2000 ($r^2 = 0.94$, $P < 0.005$) and in young growth during autumn 1998 ($r^2 = 0.94$, $P < 0.005$). However, habitat condition was independent of trap location on the grid because mean values of habitat variables in all habitats did not differ among concentric distance categories ($F = 0.35 - 2.71$, $df = 5$, $P > 0.02$).

During autumn 1998, we obtained only one significant habitat model. Vole capture in gap-phase was positively correlated ($\chi^2 = 10.04$, $df = 1$, $P < 0.002$) with percent cover of surface water, and according to the odds ratio (1.65; 95% CI = 1.04 – 2.63), a 1-unit increase in Water increased the likelihood of capturing voles by 65%. Mean percent cover of surface water was 2.1 (± 0.3) where voles were captured and 0.1 (± 0.04) at sites without captures. In contrast, mouse and vole captures in all habitats during 1999 – 2000 were significantly correlated with microhabitat variables; the only exception was Keen's mouse in peatland mixed-conifer during spring (Table 2). However, number and type of habitat correlates varied considerably among habitats and between seasons for both species. Moss was the only significant correlate of mouse captures during both seasons. Decid 4.5 and Tree 5 – 10 were significant habitat correlates of vole habitat use during spring and autumn (Table 2).

Table 2 Stepwise logistic regression models of habitat variables correlated with red-backed vole *Clethrionomys gapperi wrangeli* or Keen's mouse *Peromyscus keeni* microhabitat use in thinned young-growth (YG), peatland-scrub/mixed-conifer (PM) and gap-phase (GP) and multi-cohort (MC) old-growth western hemlock *Tsuga heterophylla* / Sitka spruce *Picea sitchensis* rain forest during spring and fall 1999 – 2000, Wrangell Island, Southeast Alaska (N/A denotes no significant model)

Model	Red-backed voles					Keen's mouse				
	Variable ^a	$P > \chi^2$	Parameter estimate (SE)	Odds ratio ^b (95% CI)	Model fit ^c	Variable ^a	$P > \chi^2$	Parameter estimate (SE)	Odds ratio ^b (95% CI)	Model fit ^c
Spring										
YG	Stump	0.01	0.01(0.01)	1.02(1.00–1.03)	$P = 0.41$	Moss	0.01	-0.03(0.01)	0.71(0.57–0.86)	$P = 0.10$
						Herb	0.01	-0.04(0.02)	0.64(0.45–0.88)	
PM	Tree 5–10	0.03	0.01(0.01)	1.02(1.00–1.03)	$P = 0.99$	Hard 10–49	0.01	0.01(0.01)	1.09(1.01–1.19)	$P = 0.63$
	Hard 10–49	0.02	0.01(0.01)	1.05(1.00–1.10)						
	Decid 4.5	0.04	0.11(0.06)	3.00(1.02–9.20)						
GP	KMcapture ^d	0.02	11.7(5.1)	1.32(1.05–1.68)	$P = 0.04$	RVcapture ^e	0.01	13.6(5.51)	1.28(1.06–1.58)	$P = 0.29$
						Moss	0.02	-0.03(0.01)	0.77(0.62–0.95)	
MC	Decid 4.5	0.03	0.06(0.03)	1.86(1.05–3.48)	$P = 0.46$	RVcapture ^e	0.01	-18.66(6.98)	0.71(0.55–0.90)	$P = 0.51$
Autumn										
YG	Vacc 4.5	0.03	-0.02(0.01)	0.78(0.62–0.98)	$P = 0.61$	Tree 10–49	0.02	-0.03(0.01)	0.97(0.95–1.00)	$P = 0.88$
PM	Decid 1	0.01	-0.15(0.06)	0.23(0.07–0.62)	$P = 0.21$	N/A				
	Soft 10–49	0.02	0.01(0.01)	1.03(1.01–1.07)						
GP	Tree 5–10	0.01	-0.01(0.01)	0.98(0.97–0.99)	$P = 0.11$	Moss	0.01	-0.04(0.01)	0.67(0.53–0.83)	$P = 0.44$
	Decid 1	0.02	0.16(0.06)	5.21(1.83–16.8)						
	Decay V	0.02	0.01(0.01)	1.01(1.01–1.04)						
	Decid4.5	0.01	-0.06(0.03)	0.53(0.32–0.87)						
Autumn										
MC	Hard 10–49	0.01	0.01(0.01)	1.05(1.01–1.10)	$P = 0.51$	Moss	0.01	-0.03(0.01)	0.73(0.58–0.90)	$P = 0.22$
	Tree 74	0.03	-0.01(0.01)	0.92(0.84–0.99)		Soft 50–74	0.01	0.01(0.01)	1.01(1.00–1.02)	
						Tree 5–10	0.03	0.01(0.01)	1.01(1.00–1.02)	

a: See Table 1 for a description of habitat variables. b: Effect of a 10 unit increase in the value of the variable (e.g., percent cover) on the probability of capture (SAS 2000). c: Hosmer and Lemeshow goodness-of-fit test (SAS, 2000), reported as the $P > \chi^2$ that the model will be improved by an additional habitat variable. d: Capture rate of Keen's mouse *Peromyscus keeni macrorhinus*. e: Capture rate of red-backed vole *Clethrionomys gapperi*.

Percent cover of deciduous shrubs explained more variation in vole captures than any other variable, as Decid 1 and Decid 4.5 were significant correlates of vole captures in two habitats during both seasons (Table 2). Furthermore, an increase of 10 units (i.e., percent ground cover) of Decid 4.5 in peatland mixed-conifer and multi-cohort old growth increased the odds of catching voles during spring by factors of 3.00 and 1.86, respectively. Mean percent cover of Decid 1 and Decid 4.5 at spring capture sites was 9.8 (± 1.4) and 5.6 (± 0.7), respectively, for peatland mixed-conifer and was 4.7 (± 0.5) and 4.8 (± 0.3), respectively, for multi-cohort; corresponding values for sites without captures were 8.7 (± 0.7) and 4.2 (± 0.4) for peatland mixed-conifer and 3.9 (± 0.3) and 2.7 (± 0.5) for multi-cohort. In gap-phase, a similar difference in Decid 4.5 decreased the odds of capturing voles during autumn by a factor

of 1.89 (1/0.53). Mean Decid 4.5 of capture sites was 4.6 (± 0.7), whereas noncapture sites averaged 5.4 (± 0.6). However, voles seemed to be most sensitive to variation in low (< 0.30 cm) deciduous shrub cover, especially in gap-phase during autumn when a projected 1-unit (%) increase of Decid1 increased the odds of capture by a factor of 5.21; mean percent cover of capture and non capture sites were 5.5 (± 0.4) and 3.8 (± 0.3), respectively. A similar difference in shrub cover in peatland mixed-conifer (capture sites $-\bar{X} = 6.3 \pm 0.7$; noncapture sites $-\bar{X} = 10.0 \pm 0.8$) decreased the odds of capturing voles during autumn by a factor of 4.35 (1/0.23).

For mice, percent cover of moss on the forest floor was the most common correlate of habitat use with significant inverse relationships in young growth, peatland mixed-conifer, and gap-phase during both seasons (Table 3). Mean values of Moss at

capture and noncapture sites during spring for young growth, peatland mixed-conifer, gap-phase, and multi-cohort were 28.0 (± 2.8) vs 39.2 (± 1.7), 72.8 (± 5.7) vs 83.2 (± 0.9), 70.4 (± 1.2) vs 75.1 (± 1.2), and 54.9 (± 1.9) vs 58.2 (± 1.7), respectively. Corresponding values for autumn captures were 34.8 (± 2.2) vs 37.4 (± 2.0), 77.9 (± 2.6) vs 83.5 (± 0.9), 69.1 (± 1.4) vs 75.3 (± 1.1), and 53.2 (± 1.7) vs 59.7 (± 1.7).

During spring, mice and vole captures were cor-

related in gap-phase; the odds of capturing voles were 32% higher at trap stations where a mouse was caught. Similarly, the odds of capturing mice were 28% higher at trap stations where voles were caught. However, spring captures of mice were inversely related to vole captures in multi-cohort; as the probability of capturing a vole at a station increased by 1-unit, the odds of capturing a mouse decreased by about 40%.

Table 3 Multivariate factors with factor loadings (>0.40) generated from factor analysis (SAS 2000) of 26 habitat variables measured in thinned young-growth (YG), peatland-scrub/mixed-conifer (peatland-MC) and gap-phase and multi-cohort old-growth (OG) western hemlock *Tsuga heterophylla*/Sitka spruce *Picea sitchensis* rain forest during 1999–2000, Wrangell Island, South-east Alaska

Factor	Thinned YG		Peatland-MC		Gap-phase OG		Multi-cohort OG	
	Variable ^a	Loading	Variable ^a	Loading	Variable ^a	Loading	Variable ^a	Loading
1	Vacc 1	0.762	Vacc 4.5	0.773	Vacc 1	0.742	Decid 1	0.742
	Vacc 4.5	0.873	Vacc 1	0.713	Vacc 4.5	0.700	Wood	-0.714
	Moss	0.726	Herb	-0.608	Tree 5–10	-0.666	Decid 4.5	0.611
			Water	-0.442	Tree 10–49	-0.606	Herb	0.451
			Stump	0.403	Conif 1	0.512	Conif 4.5	0.409
				Decid 1	0.494			
2	Decid 1	-0.605	Conif 1	0.692	Wood	0.634	Vacc 1	0.726
	Decid 4.5	0.571	Hard 74	0.620	Moss	-0.630	Vacc 4.5	0.713
	Tree 10–49	0.544	Conif 4.5	0.545	Decay I	0.495	Water	-0.488
	Wood	0.489	Decid 1	0.535	Decay II	0.495	Tree 74	-0.404
	Conif 1	-0.457	Tree 50–74	-0.520	Conif 4.5	0.490		
	Conif 4.5	-0.414	Wood	-0.476	Soft 74	0.410		
	Soft 50–74	0.437	Moss	0.452				
3	Water	-0.562	Decay II	0.875				
	Stump	0.547	Tree 74	0.838				
	Herb	-0.488	Decid 4.5	0.411				
	Conif 4.5	0.470						
	Tree 5–10	-0.427						
4			Decay III	0.8849				
			Soft 74	0.8024				

a: See Table 1 for a description of habitat variables.

Factor analysis generated three discernible orthogonal factors for young growth, four factors for peatland mixed-conifer, and two factors each for gap-phase and multi-cohort (Table 3). However, habitat factors explained little additional variation in micro-habitat use by voles or mice (Table 4). There was only one significant model during spring; a mouse capture in young growth was inversely correlated with Factor 1, which was largely understory cover of *Vaccinium* and Moss (Table 3). Vole captures during autumn also were inversely correlated with Factor 1

in young growth. Gap-phase was the only habitat where vole or mouse captures were positively correlated with any multivariate factor. A 1-unit increase in Factor 1 increased the odds of capturing voles by 82%, whereas a comparable increase in Factor 2 raised the likelihood of capturing mice by 34%. Gap-phase Factors 1 and 2 were each comprised of several variables, but were largely understory cover of *Vaccinium*, conifer seedlings, low deciduous shrub cover, amount of coarse woody debris, and downed wood in early stages of decay, respectively (Table 3).

Table 4 Stepwise logistic regression models of multivariate habitat factors correlated with red-backed vole *Clethrionomys gapperi wrangeli* or Keen's mouse *Peromyscus keeni macrorhinus* microhabitat use in thinned young-growth (YG), peatland-scrub/mixed-conifer (peatland-MC) and gap-phase and multi-cohort old-growth (OG) western hemlock *Tsuga heterophylla*/Sitka spruce *Picea sitchensis* rainforest during spring and autumn 1999 – 2000, Wrangell Island, Southeast Alaska (N/A denotes no significant model)

Model	Red-backed voles					Keen's mouse				
	Factor ^a	$P > \chi^2$	Parameter estimate (SE)	Odds ratio ^b (95% CI)	Model fit ^c	Factor ^a	$P > \chi^2$	Parameter estimate (SE)	Odds ratio ^b (95% CI)	Model fit ^c
Spring										
YG	N/A					1	0.036	-0.36(0.17)	0.70(0.49–0.98)	$P=0.27$
Autumn										
YG	1	0.029	-0.37(0.17)	0.69(0.49–0.96)	$P=0.04$	N/A				
PM	2	0.016	-0.54(0.24)	0.58(0.36–0.91)	$P=0.08$	2	0.006	-0.93(0.35)	0.39(0.19–0.76)	$P=0.01$
GP	1	<0.001	0.60(0.15)	1.82(1.36–2.47)	$P=0.50$	2	0.037	-0.33(0.14)	1.34(1.02–1.80)	$P=0.10$
MC	N/A					1	0.002	-0.55(0.18)	0.58(0.39–0.82)	$P=0.04$

a: Orthogonal, multivariate factors (factor analysis) of habitat variables (N/A=no significant factor). Factor 1 in YG was directly correlated with Vacc 1, Vacc 4.5, and Moss. For PM, Factor 2 was directly correlated with Decid 1, Conif 1, Conif 4.5, Tree 5–10, and Moss; Wood was negatively correlated. For GP, Factor 1 was directly correlated with Vacc 1, Vacc 4.5, Decid 1, and Conif 1; Tree 5–10 and Tree 10–49 had negative loadings; Factor 2 was directly correlated with Wood, Decay 1, Decay II, Conif 4.5, and Soft 74 and negatively correlated with Moss. Factor 1 in MC was positively correlated with Decid 1 and Decid 4.5; Wood had a negative loading. b: Effect of a unit increase in the value of the factor on the odds of a capture (SAS 2000). c: Hosmer and Lemeshow test (SAS 2000), reported as the $P > \chi^2$ that the model will be improved by an additional habitat variable.

The performance of habitat models in predicting microhabitat use varied widely. Generally, models based on habitat variables (Table 5) performed better than models developed from habitat factors (Table 6) in differentiating capture sites from sites without a

capture. The correct classification rate of all factor-based models was <61%; less than two-third of capture sites were identified correctly (i.e., sensitivity; Table 6). Most variable-based models identified >66% of vole capture sites (Table 6).

Table 5 Performance of logistic regression models of habitat variables in predicting microhabitat use by red-backed voles *Clethrionomys gapperi wrangeli* or Keen's mouse *Peromyscus keeni macrorhinus* in thinned young-growth (YG), peatland-scrub/mixed-conifer (PM) and gap-phase (GP) and multi-cohort (MC) old-growth western hemlock *Tsuga heterophylla*/Sitka spruce *Picea sitchensis* rain forest during spring and fall 1999 – 2000, Wrangell Island, Southeast Alaska (N/A denotes no significant model)

Model	Red-backed voles						Keen's mouse					
	Expected capture ^a	Correct ^b (%)	Sens ^c (%)	Spec ^d (%)	False positive ^e (%)	False negative ^f (%)	Expected capture ^a	Correct ^b (%)	Sens ^c (%)	Spec ^d (%)	False positive ^e (%)	False negative ^f (%)
Spring												
YG	0.46	56.8	36.4	73.9	46.1	41.9	0.29	63.3	55.1	66.7	59.7	21.6
PM	0.27	65.2	46.7	72.0	62.1	21.3	0.04	89.3	0	92.0	100	3.9
GP	0.41	55.5	48.9	60.0	54.2	37.1	0.50	55.9	49.1	62.7	43.2	44.8
MC	0.39	58.8	36.7	73.1	53.2	35.8	0.49	54.2	65.3	43.6	47.3	43.3
Autumn												
YG	0.30	59.8	58.0	60.5	61.8	22.6	0.51	58.0	79.1	36.1	43.8	37.5
PM	0.27	71.4	63.3	74.4	52.5	15.3	N/A	N/A	N/A	N/A	N/A	N/A
GP	0.58	62.7	60.6	65.6	29.5	44.9	0.42	60.9	65.2	57.8	47.4	30.2
MC	0.46	60.2	31.4	84.3	37.2	40.6	0.48	60.8	53.4	67.5	40.0	38.6

a: Expected probability of a capture based on the fraction of trap stations capturing voles or mice. b: Fraction of trap stations that were correctly classified. c: Sensitivity - fraction of capture sites that were correctly classified. d: Specificity - fraction of noncapture sites that were correctly classified. e: Fraction of trap stations predicted to capture an animal that were incorrectly classified as a capture site; dash denotes rate was not computable. f: Fraction of trap stations predicted to not be a capture site that were incorrectly classified as a noncapture site; dash denotes rate was not computable.

2.3 Habitat correlates of density

There were several apparent linear relationships between the average habitat condition across grids and the density of voles and mice (Table 7). Voles responded most positively to the amount of downed wood in decay class IV during both spring ($r^2 =$

0.87, $P < 0.001$) and autumn ($r^2 = 0.67$, $P = 0.01$), whereas density of small snags ($r^2 = 0.70$, $P = 0.006$) and percent cover of conifer seedlings ($r^2 = 0.84$, $P = 0.002$) had the most significant negative effect on population density during spring and autumn, respectively. Density of mice explained 62%

($F=9.71$, $P=0.02$) of the variation in vole density among grids during spring, but was unrelated ($r^2=0.28$, $P=0.179$) to vole abundance during autumn (Table 7). Not surprising, mouse density during spring

was positively correlated with vole density. However, the regression coefficient was larger for mice (0.891) than voles (0.694), suggesting that the response of mice to vole captures was greater than vice versa.

Table 6 Performance of stepwise logistic regression models of multivariate habitat factors in predicting microhabitat use by red-backed voles *Clethrionomys gapperi wrangeli* or Keen's mouse *Peromyscus keeni macrorhinus* in thinned young-growth (YG), peatland-scrub/mixed-conifer (peatland-MC) and gap-phase and multi-cohort old-growth (OG) western hemlock *Tsuga heterophylla*/Sitka spruce *Picea sitchensis* rain forest during spring and fall 1999–2000, Wrangell Island, Southeast Alaska (hyphen denotes no significant model)

Model	Red-backed voles						Keen's mouse					
	Expected capture ^a	Correct ^b (%)	Sens ^c (%)	Spec ^d (%)	False positive ^e (%)	False negative ^f (%)	Expected capture ^a	Correct ^b (%)	Sens ^c (%)	Spec ^d (%)	False positive ^e (%)	False negative ^f (%)
Spring												
YG	–	–	–	–	–	–	0.29	56.8	49.0	60.0	66.7	25.8
Autumn												
YG	0.30	54.4	46.0	58.0	68.5	28.1	–	–	–	–	–	–
PM	0.27	59.8	63.3	58.5	64.1	18.7	0.12	60.7	53.8	61.6	84.5	8.9
GP	0.58	57.3	62.2	50.5	36.9	50.4	0.42	50.9	41.3	57.8	58.7	42.2
MC	–	–	–	–	–	–	0.48	55.6	56.2	55.0	46.8	42.1

a: The observed fraction of total trap stations that captured ≥ 1 vole. b: Fraction of trap stations that were correctly classified. c: Fraction of capture sites that were correctly classified. d: Fraction of noncapture sites that were correctly classified. e: Fraction of trap stations predicted to capture an animal that were incorrectly classified as a capture site. f: Fraction of trap stations predicted to not be a capture site that were incorrectly classified as a noncapture site.

Mouse density also was correlated with several habitat features during both seasons. Similar to voles, Decay IV was the most significant positive correlate of mouse population density during spring ($r^2=0.78$, $P=0.004$); whereas, Decay III explained the most variation during autumn ($r^2=0.79$, $P=0.003$). Percent cover of moss and density of small snags were negative correlates of mouse density during both seasons (Table 7).

3 Discussion

Our study contributes unique information regarding the abundance of *Clethrionomys gapperi* and *Peromyscus keeni* populations relative to vegetative and structural features of four common rain forest habitats in Southeast Alaska. In addition, our findings contribute new information to a limited body of knowledge regarding the microhabitat preferences of these two species (Keinath and Hayward, 2003; Songer et al., 1997; Taylor, 1999) – it is the first study to quantify correlates of microhabitat use by *C. gapperi* and *P. keeni* populations in temperate rain forest. This information adds to our knowledge of the autecology of two endemic rodents and provides an important foundation for further ecological inquiries of each species or their interspecific interactions. *C. gapperi* and *P. keeni* are syntopic across

much of the range of Keen's mouse (Hogan et al., 1993; MacDonald and Cook, 1996). Details of their autecology and interspecific relations likely will yield further insights into understanding local and geographic distributions of these two species (Smith and Nichols 2004). In addition, the ecological information generated from our study is essential to land managers in Southeast Alaska seeking a sound, scientific basis for restoring the habitat of the Wrangell Island vole (*C. g. wrangeli*; Smith and Nichols, 2004).

3.1 *Clethrionomys gapperi* habitat use

Ecological theory predicts that animals select the best available habitat to maximize fitness and that the quality of habitats declines as population density increases (Fretwell, 1972; Morris, 1987a, b). Thus, during periods when population levels are relatively low, resources become more available and more individuals are able to occupy optimal habitat. But as population density increases, resources become depleted and animals move into suboptimal habitat because expected fitness in optimal habitat diminishes as populations approach carrying capacity (Songer et al., 1997). Thus, marginal habitats are occupied during periods when population densities are greatest, whereas optimum habitats support the largest fraction of the overall population when populations are lowest.

Table 7 Significant ecological correlates of density of red-backed vole *Clethrionomys gapperi wrangeli* and Keen's mouse *Peromyscus keeni macrorhinus* among thinned young-growth, peatland-scrub/mixed-conifer and gap-phase and multi-cohort old-growth western hemlock *Tsuga heterophylla*/Sitka spruce *Picea sitchensis* rain forest during spring and autumn 1999 – 2000, Wrangell Island, Southeast Alaska

Species/Season	Variable ^a	r^2	Parameter estimate(SE)	F value	$P > F$
Red-backed vole					
Spring					
	Conif 4.5	0.50	-0.102(0.041)	6.10	0.0484
	Moss	0.54	-0.037 (0.014)	7.11	0.0372
	Wood	0.67	0.113 (0.033)	11.94	0.0136
	Water	0.55	0.701 (0.260)	7.28	0.0357
	Soft 10 – 49	0.74	-0.015 (0.004)	16.97	0.0062
	Decay III	0.66	0.075 (0.022)	11.59	0.0144
	Decay IV	0.87	0.049 (0.008)	40.91	0.0007
	Mouse density	0.62	0.694 (0.223)	9.71	0.0201
Autumn					
	Conif 1	0.78	-0.559 (0.120)	21.57	0.0035
	Conif 4.5	0.84	-0.196 (0.036)	30.45	0.0015
	Tree 5 – 10	0.67	-0.007 (0.002)	12.04	0.0133
	Soft 10 – 49	0.62	-0.020 (0.007)	9.62	0.0211
	Decay III	0.52	0.099 (0.039)	6.39	0.0449
	Decay IV	0.67	0.064 (0.018)	12.05	0.0133
Keen's mouse					
Spring					
	Vole density	0.62	0.891 (0.286)	9.71	0.0201
	Conif 4.5	0.62	-0.128 (0.041)	9.67	0.0209
	Moss	0.60	-0.045 (0.015)	8.99	0.0240
	Wood	0.64	0.125 (0.039)	10.47	0.0178
	Soft 10 – 49	0.70	-0.016 (0.004)	13.83	0.0099
	Decay III	0.56	0.078 (0.028)	7.53	0.0336
	Decay IV	0.78	0.052 (0.011)	20.94	0.0038
Autumn					
	Decid 1	0.51	0.127 (0.051)	6.16	0.0477
	Decid 4.5	0.57	0.264 (0.094)	7.95	0.0304
	Moss	0.72	-0.077 (0.020)	15.09	0.0081
	Stumps	0.54	0.021 (0.008)	7.01	0.0382
	Tree 10 – 49	0.64	-0.007 (0.002)	10.64	0.0172
	Hard 10 – 49	0.51	-0.056 (0.022)	6.26	0.0464
	Soft 10 – 49	0.51	-0.022 (0.009)	6.32	0.0456
	Decay III	0.79	0.148 (0.031)	22.35	0.0032
	Decay IV	0.50	0.067 (0.027)	6.07	0.0489

a: Refer to Table 1 for a description of habitat variables.

In our study, vole densities were not consistently higher in late seral forests. The habitat distribution of voles varied between 1998 and 1999 – 2000, and likely was influenced by corresponding differences in population levels across the study area. Vole population densities were very high in 1998 across our study area and young growth supported a larger proportion of

the overall population than in 1999 – 2000, when population densities were lower. This redistribution of voles among habitats occurred largely because of a marked decline in vole density in young growth, which experienced a five-fold decline in population density between 1998 and subsequent years (Smith and Nichols, 2004). In contrast, vole density in gap-

phase declined by about 50%, which was the smallest yearly fluctuation in population level among three habitats (peatland mixed-conifer was not sampled in 1998). This pattern suggests that gap-phase was the highest quality habitat for *C. gapperi*, and that regenerating young-growth forest was a dispersal sink during 1998 (Nurdyke and Buskirk, 1991). This conclusion is supported further by evidence that the body mass of adults in young growth during 1998 was less than subsequent years and the fraction of adult females that were reproductively active was smaller in young growth than in other habitats (Smith and Nichols, 2004). Nurdyke and Buskirk (1991) observed lower body mass of *C. gapperi* in early seral habitats than in mature forests. In our study, percentages of reproductive females during 1999–2000 were higher in gap-phase and multi-cohort than young growth (Smith and Nichols, 2004).

Voies in our study readily moved relatively long distances (ca. 200 m) during intervals of <24 hours. As overall population size declined, some voles likely moved from suboptimal habitats into higher quality habitats, which consequently influenced density and microhabitat use in lower quality habitats. In watersheds where catastrophic disturbances from severe winter storms occur, patches of multi-cohort typically occur as a mosaic with gap-phase; multi-cohort patches in our study were on the order of 10–20 ha embedded in a matrix mostly of gap-phase. Given the effective sampling distance of voles in this study (Smith and Nichols, 2004), it is reasonable to suppose that individuals readily moved from one habitat to another as local populations fluctuate (Vickery and Rivest, 1992). Even when populations remain stable among years, local density and microhabitat use could have varied between habitats of similar vegetation and structure because of the interplay of local intra- and interspecific competition and predation (Bowman et al., 2001b).

Vole density among habitats was positively correlated with the amount of decayed downed wood during both seasons and coarse woody debris during spring. Spring vole densities also varied directly with percent cover of surface water. In contrast, vole densities were consistently lower at sites with higher percent cover of conifer seedlings (live and dead); in the spring, they were lower at sites with an abundant ground cover of moss. Coarse woody debris (CWD) has been reported as a significant correlate of vole abundance in montane coniferous forests of western North America (Keinath and Hayward, 2003; Nurdyke and Buskirk, 1991; Ucitel et al., 2003) and coniferous or mixedwood forest in the northeastern United States (Miller and Getz, 1973) and eastern Canada (Moses and Boutin, 2001; Bowman et

al., 2001a). Also, laboratory experiments demonstrated that voles preferred greater densities of vertical and horizontal cover (Wywiałowski, 1987). Keinath and Hayward (2003) reported that *C. gapperi* preferred stands with more uniformly distributed CWD, denser overstory canopy, and more *Vaccinium*. We did not measure canopy cover, but the rank of habitats corresponded directly with density of large (≥ 50 cm dbh) trees in the overstory. Unlike Keinath and Hayward (2003), vole population density in our study was not correlated with percent cover of *Vaccinium* in the understory, which across our study sites typically decreased as canopy cover increased.

Downed logs and other elements of CWD were a key habitat component for *C. gapperi*, suggesting that they are important as cover for feeding, reproduction, loafing, or runways for moving about their home range (Merritt, 1981; Wywiałowski and Smith, 1988; Orrock et al., 2000), or as important foraging habitat (Amaranthus et al., 1994; Maser et al., 1978; Rhoades, 1986). Deciduous shrub cover also is attractive to voles (Miller and Getz, 1973; Morris, 1989) and also may be important as escape cover (Wywiałowski and Smith, 1988; Vickery and Rivest, 1992), especially from avian predators, as well as an important source of food (e.g., *Vaccinium*; Keinath and Hayward, 2003). Wywiałowski (1987) emphasized the importance of habitat structure in facilitating access to resources without having to experience higher risk of predation. For that reason, we cannot account for voles appearing to avoid sites with denser cover of small snags and seedlings. However, voles may have responded to correlates of dense cover, i.e., selecting sites with features that were inversely related to conifer seedling and small snag density rather than explicitly avoiding dense cover. Small snags and seedling density were both inversely correlated with Wood or Decay IV. This also may have been the case for moss, which typically occurs on wetter sites and nutrient-poor soils (Neiland, 1971; Alaback, 1982), and in our study was indirectly correlated with Decay III and Decay IV, and to a lesser extent surface water. That vole density in our study was directly correlated with percent cover of free water is not surprising. *C. gapperi* has a high physiological requirement for water (Odom, 1944; Getz, 1962, 1968; McManus, 1974), favors mesic forests (Merritt, 1981; Orrock et al., 2000), and usually is more abundant near water or wet sites (Odom, 1944; Manville, 1949; Vickery and Rivest, 1992; Orrock et al., 2000; but see West, 1991). Orrock et al. (2000) found that vole abundance was associated with correlates of water availability and high levels of moisture at three spatial scales. Indeed, in Minnesota the local distribution of *C. gapperi* was

influenced more by the availability of free water than food*.

3.2 *Peromyscus keeni* habitat use

Young growth appeared to be the highest quality habitat for *P. keeni* as population densities were consistently the highest and changes in autumn density smallest in this habitat. Also, Smith and Nichols (2004) reported higher summer survival rates and higher percentages of reproductive females in young growth than the other habitats. Similar results have been reported for *Peromyscus* populations on Prince of Wales Island (Southeast Alaska); young (23–25 yr-old), second growth was the highest-quality habitat for *P. keeni* (Van Horne, 1981). This habitat consistently had the highest numbers and often had the highest survival rates. Mature (190+ yr) forest had lower adult densities than did young growth, but densities of *P. keeni* were similar to those in young (2–5 yr) and older (5–9 yr) clearcuts (Van Horne, 1981).

Young growth in Van Horne's (1981) study had not been thinned, but conditions were probably similar to young growth in our study because in the former, the canopy was not completely closed and the understory was near maximum production. However, the 'mature' forest in Van Horne's (1981) study was not comparable to our gap-phase or multi-cohort. Whereas most 190-yr-old coniferous forests of western North America usually attain old-growth condition, in Southeast Alaska old-growth features typically do not develop until stands are > 300 years old (Alaback, 1982; Nowacki and Kramer, 1998). Until then, the canopy remains closed with little sunlight reaching the forest floor. Not surprisingly, understory herbs and shrubs in the 190+ yr-old stand were less abundant than in old-growth stands (Van Horne, 1981). Nevertheless, evidence from Van Horne's (1981) study and ours point to young growth with open canopies as optimal habitat for *P. keeni* in Southeast Alaska. Our findings and those of Hanley and Barnard (1999) indicate that old-growth forests also support robust populations of *P. keeni*.

In our study, many features of habitat patches that were positive correlates of vole density also were important to mice. Indeed, vole and mouse density were each positively correlated with the density of the other species during spring, suggesting that there was considerable overlap in habitat preference between the two. Similar to voles, variation in mouse density across habitats was most explained by decayed downed wood during both seasons; moss cover and density of small snags and conifer seedlings were neg-

ative correlates of abundance. The habitat condition that distinguished mice from voles was deciduous shrub cover, which was positively correlated with mouse density during autumn. The reason for this difference between species is unclear; as suggested above it may be related to the positive association of voles with denser canopy cover, which on our study area was inversely correlated with shrub cover. Another possible explanation is that mice were responding primarily to local vole abundance, avoiding stands with higher vole densities during autumn. Several investigators have reported an inverse correlation in abundance among habitats or other evidence of habitat segregation between deer mice *P. maniculatus* and voles (Vickery, 1981; Healy and Brooks, 1988; Vickery and Rivest, 1992) or between *Peromyscus* species (Songer et al., 1997), suggesting further that these patterns were mediated through interspecific interactions (Vickery and Rivest, 1992). We saw a positive correlation between vole and mouse densities in the spring, but autumn population density was higher for both species, suggesting that at higher densities conspecific and interspecific interactions began to influence the habitat use of each species (Morris 1987a, b, 1996; Vickery and Rivest, 1992; Songer et al., 1997).

Microhabitat use by mice in our study was not random as has been reported for some *Peromyscus* populations elsewhere (Morris, 1984; Vickery and Rivest, 1992). We obtained significant models of single variables or multivariate factors across all habitats. Also, Wood and other elements of CWD were significant correlates of mouse density among habitats. There is no other quantitative study of microhabitat use by *P. keeni* in Southeast Alaska with which to make comparisons. What is known comes from studies in Washington, where *P. keeni* had a strong association with old-growth forests (Songer et al., 1997; Taylor, 1999). Populations in southeast Alaska seemed to be ecologically similar to *P. maniculatus* populations on the Olympic Peninsula, which in forest habitat similar to our study area were equally abundant across all seral stages (Taylor, 1999) or most abundant in clearcuts (Songer et al., 1997). Our findings and those of earlier studies indicate that *P. keeni* flourishes in a wide range of habitats, including riparian and upland old growth (Van Horne, 1981; Hanley, 1996; Hanley and Barnard, 1999; Smith et al., 2001), but is not an old-growth associate as has been observed in the southern portion of its range (Songer et al., 1997; Taylor, 1999).

3.3 Implications for conservation

* Butsch RS, 1954. The life history and ecology of the red-backed voles *Clethrionomys gapperi* Victor in Minnesota. Ph.D. Dissertation, University of Michigan. Ann Arbor, Michigan.

Throughout much of its range, *C. gapperi* has been characterized as a specialist of late-seral forest habitat (Lovejoy, 1975; Merritt, 1981; 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., 1999, 2000). Recent evidence suggests, however, that the habitat relations of species are influenced by many factors (Wiens et al., 1986; Morris, 1987a, b, 1989; Stapp, 1997; Keinath and Hayward, 2003), and that habitat affinities of species can vary between geographic regions because of environmental context (e.g., Morris, 1989), particularly the composition of small mammal communities (Smith and Nichols, 2003; Songer et al., 1997; Taylor, 1999). In many coniferous forests of western North America, *C. gapperi* may be unable to persist in clearcuts or young growth because of high physiological requirements for water (Odom, 1944; Manville, 1949; Getz, 1962; Orrock et al., 2000; Vickery and Rivest, 1992) and because of dramatic vegetative and microclimatic changes in the understory that typically accompany canopy removal. Perhaps the cooler, wetter climate of Southeast Alaska mitigates desiccation that frequently occurs following canopy removal and thus renders open-canopied, young-growth stands suitable as marginal habitat for voles. Nonetheless, voles occurred in young growth throughout our entire study; indeed, the largest number of voles captured during our study was in young growth during autumn 1998. If these results can be generally extrapolated across the range of *C. gapperi* in Southeast Alaska, vole populations may be able to persist in thinned second-growth stands, which likely would reduce the risk of local extirpation in intensively managed landscapes (USDA Forest Service, 1997).

As for *P. keeni*, evidence from our study confirms the findings of previous investigators in Southeast Alaska that endemic populations thrive in a variety of habitats ranging from recent clearcuts to old-growth forests and include riparian, upland and mixed deciduous and coniferous forests (Van Horne, 1981; Hanley, 1996; Hanley and Barnard, 1999; Smith et al., 2001). There are, however, many questions about the role of interspecific interactions in the dynamics of mouse and vole populations in managed landscapes, particularly the recovery of *C. gapperi* following catastrophic or continuous broad-scale habitat disturbance. Given their similarities in habitat relations, it is conceivable that well-established populations of *P. keeni* could add ecological interference to successful re-occupation of suitable habitat by voles, especially if the niche of *C. gapperi*

substantially overlapped and was narrower than that of *P. keeni* (Smith, 1987). This question is beyond the scope of our paper, but warrants further investigation with analyses that more explicitly test theories of habitat selection and quantify niche overlap between *C. gapperi* and *P. keeni* (Morris, 1996; Schnurr et al., 2004).

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