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Flying Squirrel Demography Varies Between Island Communities with and without Red Squirrels

Abstract

Recent studies in Southeast Alaska suggest the ecology of *Glaucomys sabrinus* differs from populations in the Pacific Northwest. In Southeast Alaska, densities were the highest reported for the species, populations were not as closely linked to old-forest attributes, and individuals had a more diverse diet that was less dependent on mycophagy. Pacific Northwest communities are comprised of several arboreal rodents; Southeast Alaska has a depauperate mammal fauna. I hypothesized that Southeast Alaska populations had a broader realized niche because of competitive release. The red squirrel (*Tamiasciurus hudsonicus*) is the only other arboreal squirrel and it is absent from the southern outer islands of Southeast Alaska's Alexander Archipelago. I compared demography and body mass of *G. sabrinus* on Prince of Wales Island to a population in sympatry with *T. hudsonicus* on a separate island (Mitkof). Home ranges were larger and population density, breeding female density, and juvenile recruitment of *G. sabrinus* were all lower in sympatry with *T. hudsonicus*. In a companion study, *G. sabrinus* on Prince of Wales Island used cavities for denning relatively more frequently than in sympatry with *T. hudsonicus* on Mitkof Island. Female *G. sabrinus* depend on cavities for natal dens, and breeding female and population densities are positively correlated with large snag or tree density. The presence of *T. hudsonicus* may influence *G. sabrinus* populations by limiting availability of cavities. Furthermore, variation in vertebrate assemblages among islands may influence realized niches of resident species, which manifest unique demographic profiles compared to populations of different ecological communities.

Introduction

The role of interspecific competition in determining distribution and relative abundance of organisms has been debated for decades (e.g., Lotka 1932, Connor and Simberloff 1979, Connell 1983, Eccard and Ylönen 2003). However, competitive interactions are widely acknowledged as a fundamental ecological process shaping vertebrate communities (Grant 1972, Cody and Diamond 1975, Sih et al. 1985, Bengtsson 1989), with direct implications for species composition and species diversity (e.g., Paine 1966). This is especially true for oceanic islands (MacArthur and Wilson 1967), where total habitat and population sizes are reduced compared to continental land areas, and thus vertebrate populations are more vulnerable to extinction from demographic stochasticity and inbreeding depression (Burkey 1995, Frankham 1998). Despite indirect evidence that interspecific competition has been responsible for exclusive distributions of ecologically similar species across island archipelagos (e.g., Conroy et al. 1999), there are few examples of island populations achieving higher densities in the absence of interspecific competitors (Crowell and Pimm 1976). Direct evidence of competitive release among insular populations would corroborate previous conclusions regarding the role of interspecific competition in structuring island communities and it would provide evidence that populations of species occupying depauperate ecological communities achieve higher densities than populations in species-rich communities.

Pacific Northwest mammal communities are diverse and comprised of several arboreal rodent species (Carey 1989, 1991, 1995), but Southeast Alaska has a depauperate mammal fauna (MacDonald and Cook 1996) with assemblages that vary among islands (Conroy et al. 1999, Smith 2005); the northern flying squirrel (*Glaucomys sabrinus*) and red squirrel (*Tamiasciurus hudsonicus*) are the only arboreal rodents in the region. *Glaucomys sabrinus* occurs on some near shore islands and a few outer islands at the southern end of the Alexander Archipelago (MacDonald and

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Cook 1996). *Tamiasciurus hudsonicus* occur on most near shore islands, but are absent from the southern outer islands; they are sympatric with *G. sabrinus* on only a few near shore islands.

Glaucomys sabrinus is a nocturnal arboreal rodent of boreal or montane coniferous forests (Wells-Gosling and Heaney 1984). Population density varies across its range and among forest types within a region (Smith et al. 2003), but typically is highest in old forests (Smith 2007) and lowest in younger or recently managed second-growth forests (Holloway and Smith 2011). *Tamiasciurus hudsonicus* is a diurnal arboreal rodent that also is common in northern and montane, late-seral coniferous forests (Steele 1998). Its density varies across regions and among forest types, but typically is highest in mature forests (Smith et al. 2003). If *T. douglasii* (an ecological equivalent; Smith 1970) is included in a comparison, geographic ranges of *G. sabrinus* and *Tamiasciurus* spp. overlap almost completely (Wells-Gosling 1984, Steele 1998, 1999). *Glaucomys sabrinus* and *Tamiasciurus* spp. use similar forest habitats, favor intact landscapes, and locally are syntopic.

There is little evidence that *T. hudsonicus* competes with *G. sabrinus*, but few studies have quantified interactions between the two species (Smith et al. 2003, Smith 2007); rather, previous investigators focused on natural history (Brink and Dean 1966, Carey 1995, Vernes et al. 2004) or responses of each species to forest structure or resource abundance (Ransom and Sullivan 2002, 2003, 2004; Ransome et al. 2004). However, there are several reasons to expect that exploitative and possibly interference competition might occur regularly between *G. sabrinus* and *T. hudsonicus*. Both species prefer cavities as nest sites (Smith et al. 2003, Edelman et al. 2009, Pyare et al. 2010) and have similar diets (Smith et al. 2003). Nest cavities can be a limiting resource for *G. sabrinus*, as females depend on cavities for rearing young (Carey et al. 1997, Carey 2002), and several investigators reported a direct relationship between population density and large tree or snag density (Carey 1995, Smith et al. 2004, Gomez et al. 2005, Lehmkuhl et al. 2006). The extent to which *T. hudsonicus* depend on cavities for denning is unclear (Smith et al. 2003, Ransome et al. 2004), but this species in these locations is typically highly territorial and residents aggressively defend resources from all intruders (Smith et al. 2003).

Despite increasing evidence that *G. sabrinus* is most abundant in old forests (Smith 2007, Smith and Holloway 2011), it seems unlikely that the reported variability in population density across its range can completely be explained by differences in forest composition or forest structure. Across mature forests of northwestern North America, population density can vary by an order of magnitude (Smith et al. 2003, Smith 2007). Recent studies of an island endemic population in coastal rainforest of Southeast Alaska suggest its population dynamics and ecology differ from populations in mesic or wet forests of the Pacific Northwest (Smith and Nichols 2003, Smith et al. 2005). Although coniferous forests of the Pacific Northwest are reputedly more productive than rainforests further north (Grier et al. 1989), mean population densities in Southeast Alaska (Smith and Nichols 2003) were the highest reported for the species (Smith 2007). Diet, in particular a lower reliance on hypogeous fungi (truffles), also differed from populations in the Pacific Northwest (Pyare et al. 2002, Flaherty et al. 2010). It has been hypothesized (Smith 2007) that higher population densities in Southeast Alaska might be due to the lower diversity of ecological communities, particularly arboreal rodents, which likely would facilitate access to a broader range of resources for island populations. Members of ecological communities often increase their distribution or relative abundance following competitive release (Cody and Diamond 1975, Sih et al. 1985, Trewby et al. 2008).

The purpose of this study is to examine the hypothesis that variation in demography and ecology of *G. sabrinus* populations in Southeast Alaska is a consequence of niche expansion resulting from competitive release. I compared *G. sabrinus* populations on two islands; one island had both arboreal squirrel species and the second only had *G. sabrinus*. My specific objectives were to: 1) compare demographic parameters of *G. sabrinus*

populations between islands; and 2) compare the body mass of *G. sabrinus* between islands. I discuss the results of my experiment in consideration of published evidence that the habitat of *G. sabrinus* in Southeast Alaska is not an emergent property of old-growth forest (i.e., synergistic outcome of essential attributes or conditions occurring coincidentally in a forest patch approaching the spatial scale of an individual home range; Smith et al. 2005); rather, populations have broader habitat and diet niches than populations in similar forest types in the Pacific Northwest. I also consider published findings of a previous companion study regarding variation between island populations in the use of a potentially limiting resource.

Study Area

I conducted this study on two islands in the Alexander Archipelagos of Southeast Alaska (Figure 1): Prince of Wales Island (55.8 °N, 132.8 °W) and Mitkof Island (56.6 °N, 132.9 °W). *Tamiasciurus hudsonicus* is sympatric with *G. sabrinus* on Mitkof Island, but does not occur on Prince of Wales Island (MacDonald and Cook 1996). Southeast Alaska has a cool, wet (200-600 cm precipitation) maritime climate with mean monthly temperatures ranging from 13 °C in July to 1 °C in January (Searby 1968). The region is unique with numerous naturally fragmented landscapes, a dynamic geological history (MacDonald and Cook 1996), and coastal temperate coniferous rainforest

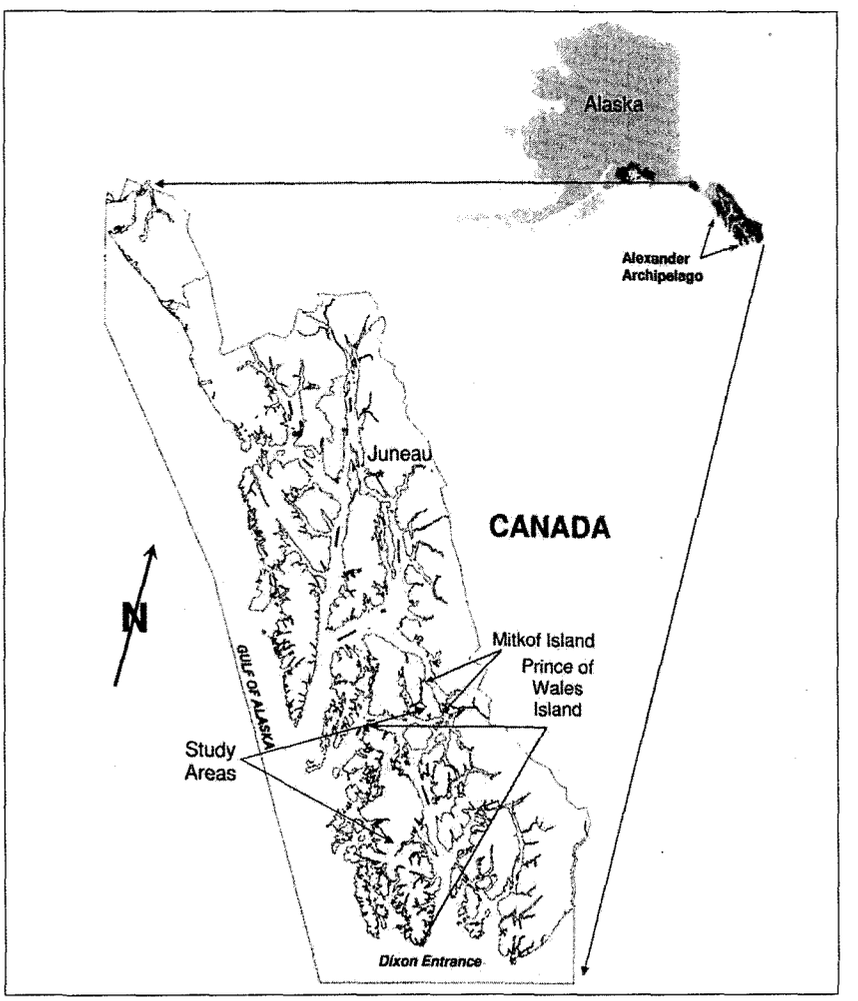

Figure 1. Location of study areas on Prince of Wales Island and Mitkof Island, Alexander Archipelago, Southeast Alaska.

(Harris and Farr 1974, Alaback 1982). Topography, geology, climate, and other environmental features create a variety of isolated habitats; heterogeneity occurs at multiple spatial scales.

Methods

I studied *G. sabrinus* populations at three upland study sites in largely unmanaged landscapes of north-central Prince of Wales Island during spring and autumn 1998 – 2000. Each site was comprised of high-volume old-growth rainforest, which has several plant associations of western hemlock (*Tsuga heterophylla*) – Sitka spruce (*Picea sitchensis*) forests (DeMeo et al. 1992); wetter sites include western redcedar (*Thuja plicata*) and yellow-cedar (*Chamaecyparis nootkatensis*). The *Tsuga-Picea* forest type comprises most of the closed canopy-forests in the region (Alaback 1982), with an uneven-aged, multi-layered overstory, dominant trees generally >300 years old, and extensive, structurally diverse understories (Hanley and Brady 1997, Ver Hoef et al. 1988). Smith and Nichols (2003) detail the study sites on Prince of Wales Island.

I studied *G. sabrinus* in sympatry with *T. hudsonicus* at two upland sites in south-central Mitkof Island (Figure 1) during spring 1998 and 2000 and autumn 2000 and 2001. The southwestern shore of Mitkof Island is about 25 km from the northeastern shore of Prince of Wales Island, separated by Sumner Strait. The forest habitats on Mitkof Island were similar to those on Prince of Wales Island; Bakker and Hastings (2002) describe the forest habitats in the landscapes surrounding my study sites. The only obvious difference between the two islands was a substantially lower percentage of redcedar in the forest canopy on Mitkof Island (Pyare et al. 2010), which is the northern limit of redcedar distribution (Pojar and Mackinnon 1994).

Demography

Live-trapping protocols followed Smith and Nichols (2003). Each grid was a 10-by-10 array of 100 trap stations at 40-m intervals (360 by 360 m) encompassing about 13 ha. One exception was a 12-by-8 grid (12.3 ha) on Mitkof Island. Two wire traps (13 by 13 by 41 cm) were placed at each station; one at a height of ~1.5 m on the bole of the largest tree within 5 m of the grid station and a second trap on or near the ground (e.g., on a downed log) within 2 m of the tree with the other trap.

I deployed trapping grids during early spring (March - April) and early autumn (September - October) because I wanted estimates of abundance immediately following winter and during the period when most reproduction and weaning had occurred but juveniles likely had not dispersed (Carey et al. 1991, Villa et al. 1999). During trapping sessions, grids usually were operated for 14 days, an initial 6-day marking period, a 2-day period when traps were closed to allow animals to recover from trap-related stress, and another 6-day recapture period (Smith and Nichols 2003). Handling and uniquely marking captured squirrels (both species) followed Carey et al. (1991) and are detailed in Smith and Nichols (2003). Live trapping and processing procedures followed guidelines established by the American Society of Mammalogists (Sikes, Gannon, and Animal Care and Use Committee 2011).

I recorded minimum number known alive (Krebs 1966), an index commonly used as a measure of relative abundance for comparative purposes (Slade and Blair 2000). I also computed a Lincoln-Petersen estimate, an unbiased estimator of population size that was selected because it affords relatively precise estimates with low biases but with relatively few assumptions or other constraints of program models (Menkens and Anderson 1988). Also, the Lincoln-Petersen estimate performs well over many different conditions and may be the best estimate of small-mammal population size (Menkens and Anderson 1988). Furthermore, I limited sampling to $\leq$ 14 days so that a closed population model could be used to estimate abundance (Carey et al. 1991). As recommended in previous studies (Otis et al. 1978, White et al. 1982), I evaluated individual behaviors and capture probabilities (Menkens and Anderson 1988) and used the procedure of Hilborn et al. (1976) to estimate recapture probability because it is the most conservative estimate among common, acceptable measures in the literature (Krebs and Boonstra 1984). Because

capture probabilities were not extremely low (< 0.1) and were relatively uniform, I used Chapman's unbiased version (Seber 1982) of the Lincoln-Petersen estimator, which generally performs better than software programs (e.g., CAPTURE; Otis et al. 1978) when sample sizes are small ($n \leq 100$; Menkens and Anderson 1988).

To obtain density (both species), I used the procedures of Wilson and Anderson (1985a) to estimate "edge effect" and effective area sampled. Mean maximum distance moved (MMDM) was estimated seasonally for each grid by averaging maximum straight-line distance between recaptures of all individuals with ≥ 2 captures. A strip equal to one-half MMDM was added as a border width to the grid to compute total area trapped (Wilson and Anderson 1985a). The strip represents the expected maximum distance beyond the grid that animals are attracted to live traps. MMDM may be biased because it can vary with number of captures (Wilson and Anderson 1985a), spacing of traps, or subsequent behavior of previously trapped animals (Carey 2000, Carey et al. 1991). Carey et al. (1991) reported that the home ranges of *G. sabrinus* determined from telemetry locations were similar to estimates obtained with mean maximum distance moved, but mean maximum distance moved likely underestimates the movements of *G. sabrinus* (Carey 2000) and ultimately the effective area trapped. Consequently, density estimates may have a positive bias, but the bias is relatively small, especially with larger (> 10 ha) grids (Carey 2000, Carey et al. 1991). Moreover, this approach seems to be preferred (Carey et al. 1991, Rosenberg and Anthony 1992, Witt 1992, Waters and Zabel 1995) because of practical considerations, such as difficulties of meeting assumptions of or obtaining sufficient number of captures required by other mark-recapture methods (White et al. 1982, Wilson and Anderson 1985b, Carey et al. 1991).

Based on evidence that flying squirrel densities on Prince of Wales Island were the highest recorded for the species (Smith and Nichols 2004, Smith 2007) and their diet was more varied and less dependent on truffles than populations in diverse arboreal rodent communities (Flaherty et al. 2010), I predicted that flying squirrel density and other population and individual attributes related to fitness would be higher on Prince of Wales than in ecological communities with other arboreal squirrel species. Therefore, I used a two-sample comparison to test the one-sided hypothesis that *G. sabrinus* density on Prince of Wales Island was higher than on Mitkof Island. For each season, I pooled estimates across years for each grid and computed mean population density and MMDM for each island population. Because I used means to obtain overall averages for each island population, I assumed the values were normally distributed (i.e., Central Limit Theorem, Zar 1999) in subsequent statistical analyses. I used a *t*-test to compare population density and a two-way analysis of variance with unequal replication (Model 1) to examine variation in MMDM between islands and seasons. I used simple linear regression to examine variation in *G. sabrinus* abundance within a grid relative to *T. hudsonicus* abundance.

I examined hypotheses regarding age and sex composition of the population with the log-likelihood ratio (i.e., *G*-statistic, Zar 1999). Mean body weight was used as an index of body condition (Dobson et al. 1999, Humphries and Boutin 2000, Larivée et al. 2010). I used a two-way analysis of variance (Model I) with unequal replication (SAS 8.1, SAS 2000) to determine if body condition of *G. sabrinus* during each season differed between islands with and without *T. hudsonicus*. I evaluated productivity by enumerating adult females during spring with evidence of recent reproductive activity, by computing the relative abundance of reproductive females expressed as a percentage of total adult females (Villa et al. 1999), and by juvenile recruitment (relative abundance of juveniles; Smith and Nichols 2003) into the autumn population. Statistical analyses were performed with SAS 8.1 (SAS 2000). I accepted $P < 0.10$ as indicating statistical significance (i.e., Type I error) because the probability of a Type II error is greater with small sample sizes (Zar 1999) and there was no compelling rationale to accept $\alpha < \beta$. Because of practical constraints of increasing sample size, the only option available to reduce β was to increase α.

Results

Minimum number of animals known alive (MNA) and population density were consistently higher during both seasons on Prince of Wales Island than on Mitkof Island (Table 1). Mean density of *G. sabrinus* on Prince of Wales Island was higher during spring ($t_{(\alpha 1),\,7} = 2.15$, $P = 0.038$) and autumn ($t_{(\alpha 1),\,9} = 1.99$, $P = 0.035$) than corresponding densities on Mitkof Island. Average density of reproductive females on Mitkof Island (0.11 ha^{-1}, SE = 0.06) was less than half ($t_{(\alpha 1),\,3} = 3.93$, $P = 0.018$) that recorded for Prince of Wales (0.30 ha^{-1}, SE = 0.02), but the proportion of females in the population that were reproductive (Table 2) was similar ($G_1 = 0.20$, $P > 0.50$). Recruitment of juveniles was higher ($G_1 = 5.1$, $P = 0.03$) on Prince of Wales (0.193) than Mitkof (0.089). Population densities of *T. hudsonicus* averaged 2.0 ha^{-1} (SE = 0.32) and 3.7 ha^{-1} (SE = 0.11) during spring and autumn, respectively.

TABLE 1. Maximum distance moved (MMDM) and 2 estimates of flying squirrel (*Glaucomys sabrinus*) abundance during spring and autumn in old-growth rain forest in sympatry with red squirrels (*Tamiasciurus hudsonicus*) on Mitkof Island and in exclusive range on Prince of Wales Island, Southeast Alaska. (Hyphen denotes values not available)

		Mitkof Island			Prince of Wales Island		
Year	Season	MNA[a] $\bar{x} \pm SD$	MMDM[b] (m) $\bar{x} \pm SD$	Density[c] (no./ha) $\bar{x} \pm SD$	MNA[a] $\bar{x} \pm SD$	MMDM[b] (m) $\bar{x} \pm SD$	Density[c] (no./ha) $\bar{x} \pm SD$
1998	Spring	2 ± 2.8	156 ± 118.8	0.3 ± 0	4 ± 1.7	142 ± 65.8	–
	Autumn	–	–	–	22 ± 3.5	76 ± 10.4	2.2 ± 0.4
1999	Spring	–	–	–	19 ± 3.5	78 ± 19.1	1.6 ± 0.4
	Autumn	–	–	–	33 ± 6.9	93 ± 8.7	4.0 ± 1.4
2000	Spring	–	–	–	20 ± 3.5	88 ± 17.3	2.0 ± 0.7
	Autumn	26 ± 4.2	133 ± 49.5	1.9 ± 1.0	30 ± 10.4	93 ± 12.1	3.4 ± 1.0
2001	Spring	12 ± 11.3	105 ± 21.2	0.8 ± 0.4	–	–	–
	Autumn	28 ± 14.1	93 ± 39.6	2.0 ± 1.1			

[a]Minimum number known alive on a grid from current and previously marked individuals.

[b]Mean maximum distance moved (Wilson and Anderson 1985*a*).

[c]Chapman's unbiased Lincoln-Petersen estimate of abundance (Seber 1982) divided by effective area sampled as estimated with mean maximum distance moved (Wilson and Anderson 1985*a*).

TABLE 2. Seasonal age and sex composition and percentage of female northern flying squirrels (*Glaucomys sabrinus*) that were reproductive in sympatry with red squirrels (*Tamiasciurus hudsonicus*) on Mitkof Island and in exclusive range on Prince of Wales Island, Southeast Alaska. (Hyphen denotes values not available)

	Spring						Autumn					
		Males		Females				Males		Females		
	N[a]	Juv[b]	Ad[c]	Juv[b]	Ad[c]	%reprod.[d]	N[a]	Juv[b]	Ad[c]	Juv[b]	Ad[c]	%reprod.[d]
Prince of Wales												
1998	11	0	6	0	5	80	65	8	25	7	25	8
1999	57	0	28	0	29	75	100	10	47	6	37	0
2000	60	0	36	0	24	75	89	8	35	10	36	0
Mitkof												
1998	5	0	4	0	1	0	–	–	–	–	–	–
2000	–	–	–	–	–	–	25	2	10	4	9	0
2001	22	0	14	0	8	75	54	1	32	0	21	0

[a]Total number of animals for which age and sex were recorded.

[b]Young of the year (i.e., age class I) according to Villa et al. (1999).

[c]Individuals that showed pelage or rostrum features of adults (Villa et al. 1999), regardless of evidence of reproductive maturity.

[d]Percentage of females exhibiting evidence of reproductive activity (i.e., in estrus, pregnant, lactating). Because data were not obtained for all adult females, sample size is ≤ number of adult females recorded.

TABLE 3. Seasonal body mass[a] (g) of juvenile and adult northern flying squirrel (*Glaucomys sabrinus*) in old-growth rainforest in sympatry with red squirrels (*Tamiasciurus hudsonicus*) on Mitkof Island and in exclusive range on Prince of Wales Island, Southeast Alaska. (n = number of squirrels) (asterisk denotes significant difference [$P < 0.10$] between islands).

	Adult				Juvenile[b]	
	Male		Female		Male	Female
	Spring*	Autumn*	Spring*	Autumn*	Autumn*	Autumn*
Location	$\bar{x} \pm SD$ n	$\bar{x} \pm SD$ n	$\bar{x} \pm SD$ n	$\bar{x} \pm SD$ n	$\bar{x} \pm SD$ n	$\bar{x} \pm SD$ n
Prince of Wales	131 14.2 38	122 14.2 70	125 21.930	122 20.3 78	107 21.5 25	110 11.3 22
Mitkof	145 12.4 16	131 13.9 40	145 10.412	138 20.1 28	115 17.5 3	99 11.6 4

[a]Based on the mass of individuals at their first capture during a trapping session (Smith and Nichols 2003).

[b]Age-class I (i.e., young of the year—Villa et al. 1999).

Also, the radius of MMDM was consistently larger ($F_{1,484} = 58.9, P < 0.001$) for *G. sabrinus* on Mitkof than Prince of Wales during both seasons (Table 1). At the scale of individual study sites, there was a positive relationship between the abundance of both species obtained during spring and autumn on Mitkof Island, with 76% of the variation ($r^2 = 0.76$) in *G. sabrinus* abundance across a grid explained by *T. hudsonicus* abundance.

The *G. sabrinus* population on Mitkof was male biased ($G_1 = 5.4, P = 0.03$), especially during spring (Table 2); on Prince of Wales, sex ratios did not depart from unity ($G_1 = 0.4, P > 0.25$). The body mass of adult *G. sabrinus* (Table 3) was greater on Mitkof Island than on Prince of Wales Island (two-factor ANOVA with unequal replication) for males and females during spring ($F_{1,92} = 7.1, P = 0.002$) and autumn ($F_{1,212} = 7.4, P = 0.015$). Mean body mass of juvenile females was greater ($t_{24} = 6.13, P < 0.001$) and juvenile males were smaller ($t_{26} = 2.4, P < 0.05$) on Prince of Wales than on Mitkof (Table 3).

Discussion

The data suggest that *G. sabrinus* demography in sympatry with *T. hudsonicus* was different than populations in an ecological community where *T. hudsonicus* was absent. Mean population density, reproductive female density, and juvenile recruitment of *G. sabrinus* were all higher and individual home ranges smaller on Prince of Wales than on Mitkof; population and reproductive female density were consistently higher in all comparisons of corresponding seasons. Population densities of *T. hudsonicus* on Mitkof were comparatively high and near the upper end of values (0.2 – 3.9 ha^{-1}) reported for this species (Smith et al. 2003).

I made at least 3 assumptions in comparing *G. sabrinus* populations between islands. The first was that replicates on each island were not spatially correlated; two sites on Prince of Wales Island were within 2 km and it is possible the estimates were not independent. However, patterns of seasonal and annual variation within sites were not consistent among sites, with one population increasing from one year to the next while others decreased. The extent to which significant differences in spring or autumn population density occurred among sites also varied annually. On Mitkof Island, there was no evidence of collinearity between *G. sabrinus* populations, which were separated by13 km. Secondly, not all density estimates were obtained during the same years and thus attributing significant variation between islands to differences in ecological communities required an assumption that local, annual demographic variation did not confound comparisons. Still, mean autumn population densities on Prince of Wales Island in 2000 were nearly twice that observed on Mitkof Island during the same year. Lastly, I assumed that the two islands in this study were representative of populations of these taxa on other islands in which *G. sabrinus* and *T. hudsonicus* occur sympatrically or *G. sabrinus* occurs exclusively.

If *G. sabrinus* demography on Mitkof Island differs from populations on Prince of Wales, then the most parsimonious explanation is that differences in habitat underlie the variation in population dynamics. Clearly, landscapes of Southeast Alaska are heterogeneous and considerable variability exists in vegetation communities at scales ranging

from tens of meters to entire watersheds (DeMeo et al. 1992). However, except for the reduced presence of western redcedar in the canopy on Mitkof Island, there were no obvious differences in forest habitat between the islands (Bakker and Hastings 2002, Pyare et al. 2010); certainly, no greater variability than exists among watersheds within an island (Smith and Nichols 2003).

Alternatively, differences in demography between islands may have been a consequence of competitive release. That is, *G. sabrinus* populations on Prince of Wales have greater access to more resources because *T. hudsonicus* is absent. Indeed, MMDM was consistently smaller, suggesting individuals needed smaller home ranges to meet their needs. To be certain, however, further study of *G. sabrinus* home range should occur on Mitkof Island and Prince of Wales Island. Niche shifts commonly are cited as evidence of changing competitive interactions (MacArthur 1972, Wiens 1989). That *G. sabrinus* respond to less interspecific competition is supported by two additional lines of evidence. Unlike populations in the Pacific Northwest, the habitat of *G. sabrinus* in Southeast Alaska is not an emergent property of old-growth forest (Smith et al. 2005). Also, and perhaps not unrelated, they have a broader realized food niche and lower reliance on fungi compared to *G. sabrinus* populations in more diverse arboreal rodent communities elsewhere (Smith 2007, Flaherty et al. 2010). Lichens and conifer seeds were the two most common items in the diet of *G. sabrinus* on Prince of Wales Island during both spring and autumn; relative contributions to the diet of *G. sabrinus* was an order of magnitude greater than fungi and much greater than that reported in more diverse ecological communities elsewhere (Smith 2007, Flaherty et al. 2010).

The necessary conditions for interspecific competition are that species must share resources and the combined exploitation of those resources or the interference interactions related to exploiting those resources must negatively affect either or both species (Wiens 1989). That *T. hudsonicus* and *G. sabrinus* are ecologically similar and share resources is supported by geographic ranges and habitat distributions that overlap almost entirely (Wells-Gosling and Heaney 1984; Steele 1998, 1999). At a finer scale, *T. hudsonicus* and *G. sabrinus* in this study appeared to prefer similar habitat as portions of a grid where *G. sabrinus* was more abundant also had higher *T. hudsonicus* abundance. A positive relationship between the densities of two species indicates each is responding to similar habitat features or resources (Morris 1987). Indeed, several investigators have reported substantial diet overlap (Brink and Dean 1966, Smith et al. 2003, Vernes et al. 2004) between *T. hudsonicus* and *G. sabrinus* and the two species respond similarly to increases in a similar food resource (Ransome and Sullivan 1997). In my study, juvenile females on Prince of Wales Island were larger than juvenile females that were sympatric with *T. hudsonicus* on Mitkof Island. However, whether competition for food was largely responsible for the variation in demography that occurred between Prince of Wales and Mitkof Island in this study remains unclear and requires additional studies of *G. sabrinus* and *T. hudsonicus* diets on Mitkof Island.

An equally critical and potentially limiting resource is suitable cavities, especially for *G. sabrinus* (Smith 2007). Females require cavities for natal dens, presumably for protection against predators (Wilson and Carey 1996). In landscapes near this study, *G. sabrinus* denned almost exclusively in cavities; only 2% of 118 den locations (34 males, 30 females) could have possibly occurred in external nests (Pyare et al. 2010). In sympatry with *T. hudsonicus* (Mitkof Island), *G. sabrinus* used external nests relatively more often, with as many as 27% of 76 dens possibly being dreys (Bakker and Hastings 2002). On at least one occasion, a *T. hudsonicus* chased a *G. sabrinus* from preferred habitat (V. Bakker, personal communication); in the Pacific Northwest, Douglas' squirrels aggressively displace *G. sabrinus* from cavities (T. Wilson, personal communication).

If *T. hudsonicus* limits the availability of cavities, then *G. sabrinus* females may be forced to use external nests with consequences for individual fitness and population demography. The abundance and distribution of large trees and snags clearly influences *G. sabrinus* behavior and demography (Smith 2007). In a previous study at the same location, the odds of catching *G. sabrinus* at microsites on Prince of Wales Island increased

17-fold with every increase of 10 large trees or snags/ha (Smith et al. 2004). It was also reported that 65% of the variation in population density was attributable to the density of large diameter (≥ 74 cm) trees and snags. Old-growth forests with large tree and snag densities that averaged an order of magnitude greater than wetter, poorly drained sites had a greater percentage of adult females in the population, a higher density of reproductive females, higher juvenile recruitment, and a higher intrinsic rate of growth (Smith and Person 2007). In fact, numerous studies across the range of *G. sabrinus* have established a direct relationship between population density and large diameter trees (Gomez et al. 2005, Lehmkuhl et al. 2006) and large snags (Carey 1995, Carey et al. 1999, Holloway and Malcolm 2006). Retaining snags in logged stands reduces disparity in population density between mature and second-growth forests (Rosenberg and Anthony 1992, Carey 1995).

Further study is needed to confidently conclude that *T. hudsonicus* directly influences the demography of *G. sabrinus* populations in Southeast Alaska. Indeed, the unexpected finding that adult *G. sabrinus* on Mitkof Island were heavier (not smaller) than individuals on Prince of Wales suggests the island populations differ in other ways that might affect their ecology or demography. Ideally, a replicated experiment comparing the demography of *G. sabrinus* on multiple islands with and without *T. hudsonicus* can more completely examine the ecological interactions between the two species. Still, the findings of multiple studies indicate *G. sabrinus* in Southeast Alaska differ in important ways from populations further south; higher population density, less reliance on old-growth forests, and a more general diet all point to a shift in niche dimensions typically associated with competitive release. The findings of my study further suggest that variation among islands in vertebrate assemblages likely produce unique demographic profiles for populations of different ecological communities. The extent to which conspecific populations vary between islands will depend on differences in island size and the species composition and diversity of communities (MacArthur and Wilson 1967). Nevertheless, recognizing that island populations can often occur in unique ecological communities, vary in demographic attributes, and likely respond differently to natural or anthropogenic disturbance is fundamental to appreciating and conserving the complexity of island archipelagos.

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