Distribution of Invertebrates Affects Territory Structure of Song Sparrows (*Melospiza melodia samuelis*) in China Camp State Park, Marin County, California

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Abstract Previous studies on marsh bird territory placement have assumed a mainly resource-based bird foraging behavior centered in defended areas along channels, with little foraging focused on food resources of the undefended high marsh plains. The theory is based on the extremely high productivity of *Spartina foliosa*, the native cord grass that dominates tidal marsh channels in the San Francisco Bay Area. Recent observations of a San Pablo Bay song sparrow subspecies, *Melospiza melodia samuelis*, in a California tidal salt marsh have shown foraging behaviors contradictory to those expected; birds are foraging outside of their defended territories in an area considered to be fairly unproductive. This study examines the distribution of invertebrates in the same marsh in an attempt to explain observed *Melospiza* foraging behaviors. Invertebrate order richness, order diversity, and community biomass composition were examined across three microhabitats: channel, high marsh plain, and *Grindelia* strips which line the channels. Over a period of four months, invertebrates were sampled by several methods including snail quadrats, pit trapping, and sweep netting, in order to obtain a representative sample of the population. Results showed a trend toward higher abundance of high-biomass species, especially *Traskorchestia traskiana*, in the high marsh plain, while a trend toward high abundance of low-biomass species, especially *Prokelisia marginata* and Diptera: Dolichopodidae, is seen in the channels. These patterns suggest *Melospiza's* foraging behavior is resource-based, as was previously thought, but that the high marsh plain is more rich in song sparrow prey items than slough channels, contrary to current belief. The data further suggest that food resources in the high marsh plain do not require defense against competitors because they are so abundant.

Introduction

Tidal salt marsh ecosystems, including those found in China Camp State Park in Marin County, California, are considered very valuable areas for bird and other wildlife habitat. In recent years, a growing amount of research has focused on identifying the basics of wetland community structure in order to form a foundation of understanding upon which to base decisions about restoration and conservation. However, while some systems have been studied intensively, a number have been neglected. The study of San Francisco Bay Area wetland invertebrates, for instance, seems to have been given very low priority during the planning and researching of restoration projects (Maffei 2000). As a consequence, very little is known about the distribution of invertebrates in tidal salt marshes. The neglect of this ecologically important group is surprising, given that invertebrates (especially insects) are not only considered excellent bioindicators of environmental stress (Hellawell 1978), but also are essential components of food web interactions and therefore contribute to overall habitat stability.

An important salt marsh group that depends in large part on invertebrate populations and that may be affected by invertebrate distribution is the large bird community at China Camp, including the seasonally-insectivorous song sparrow, *Melospiza melodia samuelis.* During their breeding season, usually from April through August (Baicicich and Harrison 1997), the diet of song sparrows shifts to include more insects (Nice 1937), in order to accommodate the protein needs of the egg-producing female, and later to help feed growing young. At the beginning of this season, male birds of breeding pairs begin to defend their territories vigorously (Nice 1941), excluding through song and aggression conspecific individuals from the established breeding territory limits. This territory, thought to facilitate pair formation between birds, regulate population density, reduce loss to predators, and preserve food resources (Van Tyne and Berger 1976), may take one of several forms. Current ornithological theory considers song sparrows to be a classic example of birds which maintain territories categorized by Tinbergen (1939) as "type A." The type A territory is a large, exclusive breeding area within which courtship and copulation, nesting, and food foraging all occur (Tinbergen).

In China Camp, song sparrow territories are defended as aggressively as elsewhere, but the structure, as well as the functionality, of the spaces deviates from the classic example. In the tidal salt marsh of this state park, song sparrows have been observed to primarily forage for invertebrates outside of their defended territories (Grenier and Beissinger, unpublished data). Furthermore, these undefended foraging areas tend to overlap, indicating sharing of food resource spaces, and even greater divergence from previously held notions about song sparrow interactions.

Several factors that influence territory structure and location may be used to explain this anomaly; proportion of females in the population, quality and availability of nesting sites, heavy predation while foraging, and high food availability may be a few (Nice 1941; Post 1974; Verner 1977). A number of features related to food distribution and differences in quality may be important issues when considering effects on bird positions in the marsh. For instance, many birds value a varied diet, consisting of a high diversity of items (Barrantes and Loiselle 2002; Cromrich et al. 2002). However, when a particular prey item is very abundant, bird diets show trends toward less selectivity and variety (Kaspari and Joern 1993). Also, in keeping with basic ecological foraging theory, birds tend to select prey that has a higher nourishment return for the energy spent obtaining it (Kaspari and Joern), implying a balance between capturing difficulty and nutrient content of the prey. In this study these two factors will be considered qualitatively—capturing difficulty will correspond to ease of catch and handling, especially referring to invertebrates that do not fly or burrow and that do not have hard outer shells, and nourishment will be roughly related to biomass, where invertebrates with higher biomass will be regarded as more rewarding catches.

This study will examine the relationship between invertebrate distribution and foraging patterns in an effort to suggest possible explanations for the deviation of these song sparrows from territorial patterns observed elsewhere. This will be achieved through the meticulous sampling of invertebrates in the song sparrow-occupied tidal salt marsh area in China Camp. Because the habitat structure is fairly homogeneous for each microhabitat in the marsh, and the preferred foraging areas are dominated by vegetation that can be considered less structurally complex relative to other habitat structures in the marsh, the data from the invertebrate survey is expected to show lower diversity in the preferred foraging areas than in the defended areas. This difference is hypothesized to be compensated for by a high abundance of high-biomass, easy-capture prey in the areas where song sparrows have been observed foraging, and a lower abundance of high-biomass, easy-capture prey in areas within the defended territory.

Methods

Study Site Invertebrate samples were taken in a tidal salt marsh at China Camp State Park, Marin County, California (38º00'45" N, 122º29'25" W). China Camp salt marsh covers an area of approximately 180 ha along the southwestern edge of San Pablo Bay (the northern portion of San Francisco Bay; Fig. 1). The climate is temperate, with moderate rainfall occurring almost exclusively in the winter (of the 700mm/year average, only 20 mm fall between May and September). This study site covers an area of about 5,500 m^2, and has no freshwater inflow from upland. Water from San Pablo Bay enters the marsh via one large slough that branches into several smaller secondary and tertiary

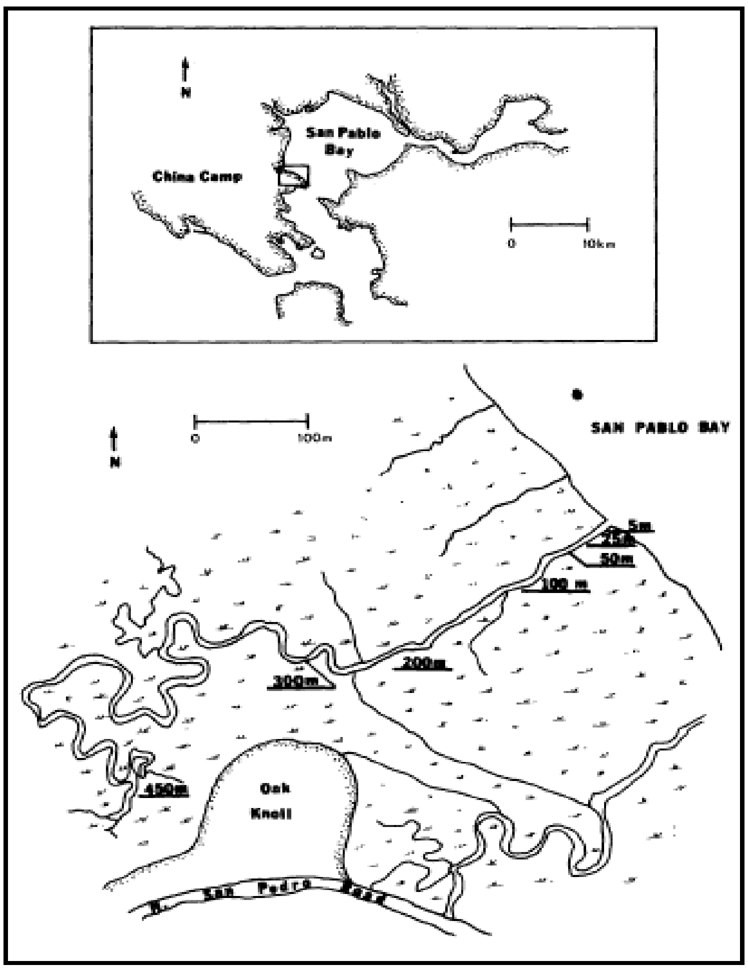

Figure 1. Map of study site in China Camp State Park, Marin County, California. Water flows from San Pablo Bay into the site through large slough channels off of which several smaller channels branch. The flow system allows for the occasional inundation of mid-level areas, the pickleweed-dominated marsh plain. From Hopkins and Parker (1984).

channels. The marsh displays vegetation typical of undisturbed salt marsh, with low overall species diversity. Along each channel, striking zonation of vegetation is evident, a common characteristic of tidal salt marshes (Monroe and Olofson 1999; Mahall and Park 1976) that has been shown to affect the distribution of invertebrates (Cameron 1972). This specific marsh system is divided into three main vegetation zones: area dominated by the tall cord grass, *Spartina foliosa,* in low marsh between about 0.34m above MLLW (Mean Lowest Low Water) and MHW (Mean High Water, at about 1.8m above MLLW in this area of San Francisco Bay (Pestrong 1972)); area dominated by a low-growing succulent, *Salicornia virginica* (pickleweed), on the marsh plain (the vast majority of the land area), at elevations near and above MHW, eventually intergrading with the upland vegetation; and thin strips of tall brush, *Grindelia humilis,* that line all of the large channels and most of the smaller channels along the marsh plain, representing the highest elevation on the marsh plain (Fig. 2). Other more minor plant species are *Distichilis spicata*, *Limonium californicum*, *Jaumea carnosa*, and *Frankenia grandifolia,* which are found primarily along channels and along the channel side of the *Salicornia* stands above MHW. The areas being strongly defended by song sparrows are the spaces along the tidal channels, including the "slough" microhabitat (as it will be referred to for

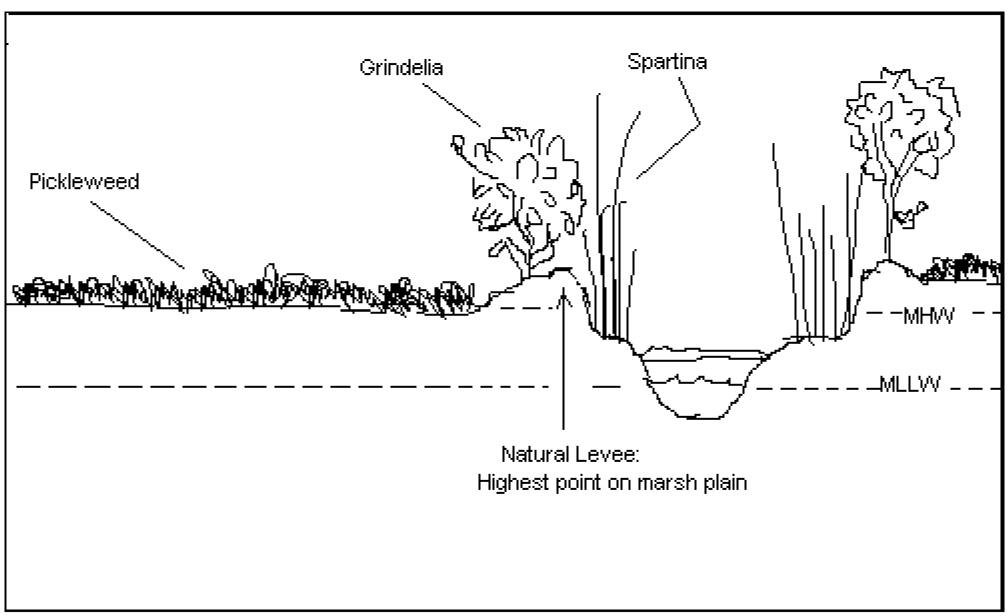

Figure 2. Vertical and vegetal zonation of the tidal salt marsh. Notice that although the *Grindelia* strips lie close to the channels, inundation of the land they occupy occurs less frequently because of the natural levee produced by years of sedimentation. (MHW is Mean High Water; MLLW is Mean Lowest Low Water.)

the remainder of this paper) and the *Grindelia* microhabitat; foraging is observed on the undefended marsh plain, hereafter referred to as the pickleweed zone.

Field Sampling Design and Methods Between May and August 2001, 9 samples were taken from or near each of 24 song sparrow territories that had been observed in the same location for two years before invertebrate collection began. Twelve territories abutted the large sloughs in the study system and twelve lined small sloughs. During any given sampling day, large and small sloughs received equal sampling effort. Of the nine samples taken per territory, three were in the *Grindelia* microhabitat, three were in the slough microhabitat, and three were in the pickleweed microhabitat, outside of the defended territory. Random sampling along both an x- and y-axis for each territory was used; three separate y-axes at random points along a single x-axis each contained one sample in each vegetation zone. Though questions of the study appear to involve only two types of areas, those defended and those not defended by song sparrows, it is important to recognize the complexities presented by the discrete vegetal zonation characteristic of tidal salt marshes. Of the three microhabitats described here, song sparrows defend both the area with the highest degree of tidal inundation (the slough zone) and the area with the lowest degree of inundation (the *Grindelia* zone). Combining the two distinct microhabitats would yield an inaccurate representation of the bird territory.

Because of the varied nature of invertebrate motion and habitat choice, no single method was appropriate for representative sampling. Therefore, the method of choice was a compilation of several methods, designed to include the many functional groups of invertebrates that might be targeted as prey by sparrows. Pit trapping, sweep netting, and snail quadrats were utilized. Pit traps were 32-oz (11cm diameter mouth and 13 cm deep) plastic containers which were placed into the ground so that the mouths were flush with the ground and there was no discontinuity between the edge of the trap and the ground surface. The net used for sweep netting had a resilient wire mouth with a diameter of 48 cm. A sample consisted of 10 strokes, 180º around the sweep netter. Because sweep netting has been noted to have biases associated with changes in cloud cover and wind (Cameron 1972), sweep netting was performed only on sunny days with little to no wind. Snail quadrats were square PVC frames with side lengths of 22 cm that were placed at random locations in the sample sites. Snails within the square were counted and recorded. Invertebrates caught in pit traps or sweep nets were also counted. Common taxa were defined as those caught at least 10 times by a given method.

Invertebrates caught through sweep netting and pit trapping were brought back from the field and kept alive up to 24 hours to allow gut evacuation for accurate weighing. They were then rinsed with deionized water and placed in an oven to dry at 60º until they maintained constant weight. Biomasses of dried samples were taken at mg level with an Ohaus Analytical Plus Scale. Invertebrates that were not dried were placed in 70% EtOH and were identified to order with the help of Borror's *An Introduction to the Study of Insects* (1989) and several invertebrate identification specialists on the University of California at Berkeley campus.

Statistical Analyses Several comparisons were made in order to determine the level of diversity differences between the three microhabitats discussed in the previous sections. The Simpson Index, calculated as

$$\lambda = 1 - \Sigma\, ((n_i/n)^2),$$

where n_i is the number of individuals of taxon i and n is the total number of individuals, was used to approximate diversity because it communicates evenness of a community. This is important when considering measures of diversity that are practical in relation to bird diets; if a specific item is collected only rarely, it would be impractical to weight that individual's taxon in the same manner as other, more commonly collected, items. However, in an effort to show relative richnesses of the microhabitats, simple richness numbers (i.e. the number of orders collected during each trapping) were compared between the three zones as well.

When considering modes of comparison, it was necessary to investigate the normality of the data distribution in order to decide which tests, parametric or non-parametric, would give the strongest significance estimates with the least chance of error. ANOVA (Analysis of Variance) tests for the equality of the means of several univariate samples, and assumes a normal distribution. ANOVA is robust to heterogeneity of samples as long as all sample sizes are equal or nearly equal. In order to test a null hypothesis of normality, the squares of the Kurtosis values of each variable set (grouped by zones) were correlated with the χ^2 distribution for two degrees of freedom in order to find the probability that the K^2 value of that set would occur in a normal distribution. According to Zar (1999), this normality test works well for $n > 20$. For all data sets with squared

Kurtosis values indicating a $p > 0.05$, normality was assumed and an ANOVA was performed for that set. All other sets were assumed to have non-normal distributions and Kruskal-Wallis analyses, which have a strength $3/\pi$ times (about 95%) that of ANOVA, were performed. Significant difference between sets was defined as having $p < 0.05$.

Results

Comparison of Common Taxa across three Microhabitats Ten orders of invertebrates were found which could be considered viable prey items: Araneae (spiders), Amphipoda (amphipods), Basommatophora (snails), Coleoptera (beetles), Diptera (flies), Hemiptera (true bugs), Homoptera (hoppers, aphids, etc.), Hymenoptera (bees and wasps), Lepidoptera (butterflies and moths), and Orthoptera (grasshoppers). Common taxa, defined above as any invertebrate group that was sampled more than 10 times by a given method, were identified beyond order and are listed in Table 1. The amphipod, *Traskorchestia traskiana*, was the heaviest of all prey items collected quantitatively, while the plant hopper, *Prokelisia marginata* was the lightest (Fig. 3); *T. traskiana* weighed in with a mean dry mass approximately 30 times greater than that of *P. marginata*.

One trend in prey distribution elucidated by this survey is shown in figures 4 and 5; groups of invertebrates that travel on the ground, such as amphipods, wolf spiders (family *Lycosidae*), and bronze beetles (Coleoptera: Carabidae) were rarely found in the slough zone, and most were significantly abundant in the Pickleweed zone (Table 2).

Phylum	Class	Order	Family	Genus	Species	Common
Arthropoda	Crustacea	Amphipoda	Talitridae	Traskorchestia	traskiana	Amphipod
Arthropoda	Insecta	Coleoptera	Carabidae	Bembidion		Bronze Beetle
Arthropoda	Insecta	Diptera	Dolichopodidae			Fly
Arthropoda	Insecta	Diptera	Otitidae	Seioptera		Fly
Mollusca	Gastro-poda	Basomma-tophora	Ellobiidae	Myosotella	myosotis	Snail
Arthropoda	Arachnida	Aranea	Lycosidae			Wolf spider
Arthropoda	Arachnida	Aranea	Araneadae			Orb spider
Arthropoda	Insecta	Homoptera	Delphacidae	Prokelisia	marginata	Plant hopper

Table 1. Commonly captured mature invertebrates identified to various taxonomic levels. Diptera: Dolichopodidae, Aranea: Lycosidae and Araneadae could not be identified past family without dissection. Invertebrates identified to species level are recognized as fairly common residents of Marin salt marshes.

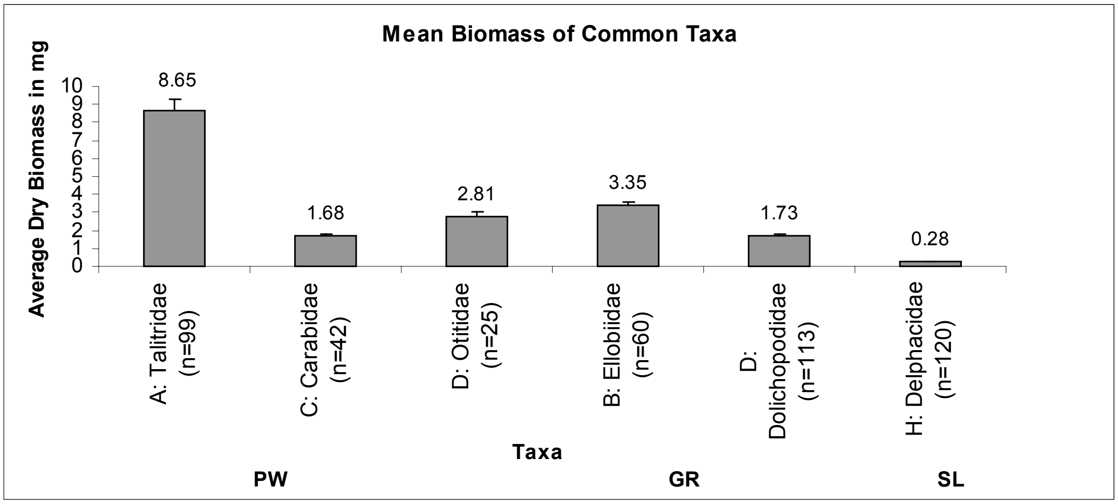

Figure 3. Mean dry biomasses of commonly-captured taxa. Notice that the average mass of the three taxa at the left of the figure (common in the pickleweed zone) is much higher than elsewhere, especially the slough zone. PW stands for pickleweed, GR for *Grindelia*, and SL for slough microhabitat.

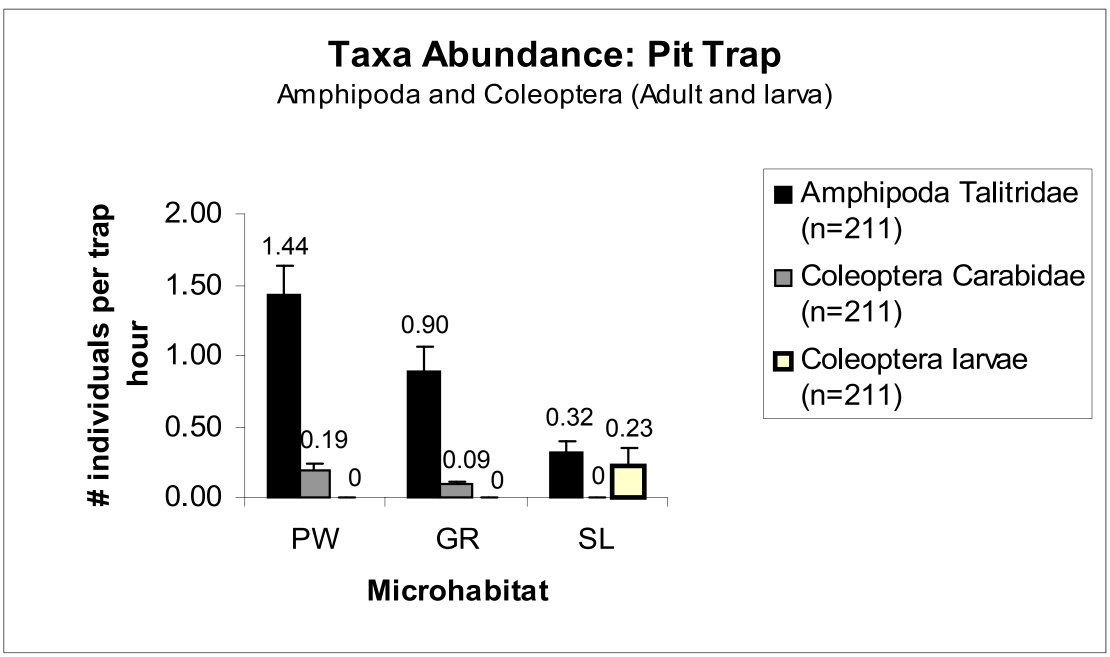

Figure 4. Taxa abundance by pit trap. The Coleoptera larvae caught in pit traps was aquatic and therefore was only found in the slough, where standing water often remains long after tide has gone out. Though amphipods were found in all three zones, they are significantly more abundant in the pickleweed zone ($p<0.001$, χ^2, df=2). Carabid beetles were not significantly more abundant in the pickleweed than in either of the other two zones ($p=0.157$, χ^2, df=2).

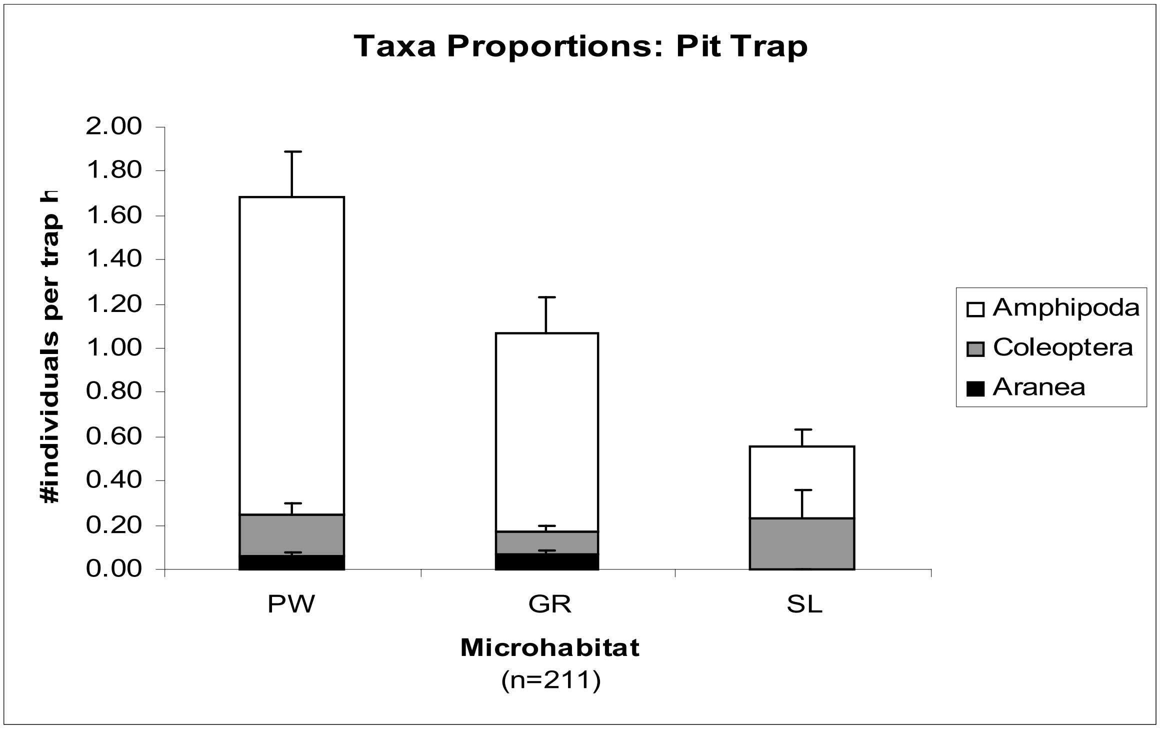

Figure 5. Proportions of total walking and crawling invertebrates caught in pit traps in the three microhabitats. This figure shows the relative proportion of the major taxa caught in pit traps. It also clearly shows that amphipods are very abundant not only in the pickleweed, but across all three microhabitats, though it is obviously most abundant in the pickleweed. Coleoptera and Aranea in this figure include all beetles and spiders caught in pit traps during the survey period.

Invertebrate	Zone of Highest Abundance	p-value
T. traskiana	Pickleweed	< 0.001
Aranea Lycosidae	Pickleweed and *Grindelia*	= 0.001
Diptera Otitidae	Pickleweed	= 0.002
Coleoptera Carabidae	Pickleweed	= 0.157
Aranea Araneadae	*Grindelia*	= 0.001
M. myosotis	*Grindelia*	< 0.001
Coleoptera larva	Slough	= 0.018
Diptera Dolichopodidae	Slough	= 0.031
P.marginata	Slough	< 0.001

Table 2. Significance of abundance in specific zones. P values were obtained from Kruskal-Wallis One-Way Analysis of Variance, assuming χ^2 distribution with df = 2. Notice that the abundant species in the pickleweed zone are primarily high-biomass, ground-traveling invertebrates, while those in the slough area tend to be lighter, flying or swimming invertebrates.

While the trend toward heavier, ground-dwelling invertebrates in the pickleweed zone, where song sparrows are feeding in undefended areas, is evident, there is a simultaneous, opposite trend toward the slough zone that should not go unnoticed (Fig 6). Not only is the higher abundance of flying invertebrates toward the channel apparent, but also the obvious decrease in biomass can be seen, especially if one keeps Figure 3 in mind while examining Figure 7.

The plant hopper, *P. marginata*, is very abundant in the slough zone and is found almost exclusively in this section of song sparrow-defended territory. In fact, it is the single most abundant invertebrate obtained with the sweep net method, caught in numbers nearly ten times those of the flies caught the same way in the same place, at a average of 9.54 individuals per sweeping. *P. marginata* is also the lightest of the more commonly caught invertebrates. The next abundant invertebrate in the slough caught via this method is Diptera Dolichopodidae, which has a mean mass more than six times greater than the plant hoppers, but is still the third lightest of the mature common invertebrates encountered in this survey.

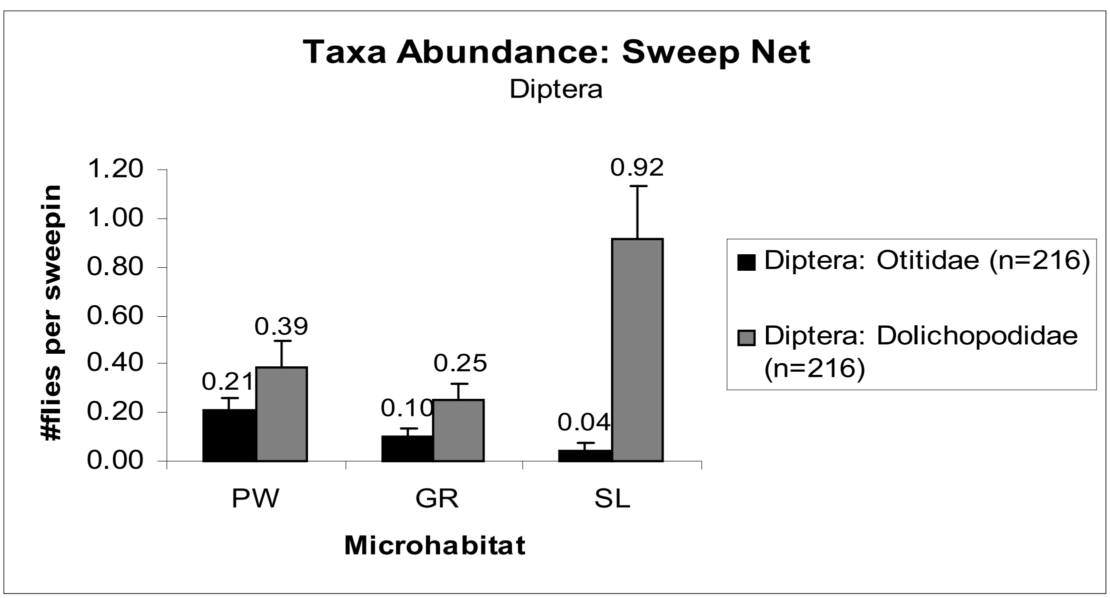

Figure 6. Taxa abundance by sweep net. These data were quite unexpected; one fly family is actually quite abundant in the Pickleweed, while it is obvious that the other fly is significantly ($p = 0.031$) more abundant in the slough. The high standard error for *Dolichopodidae* (0.22 individuals per sweeping) in the slough is probably the result of a very patchy distribution of this fly, compared with the slightly more uniform distribution of *Otitidae*.

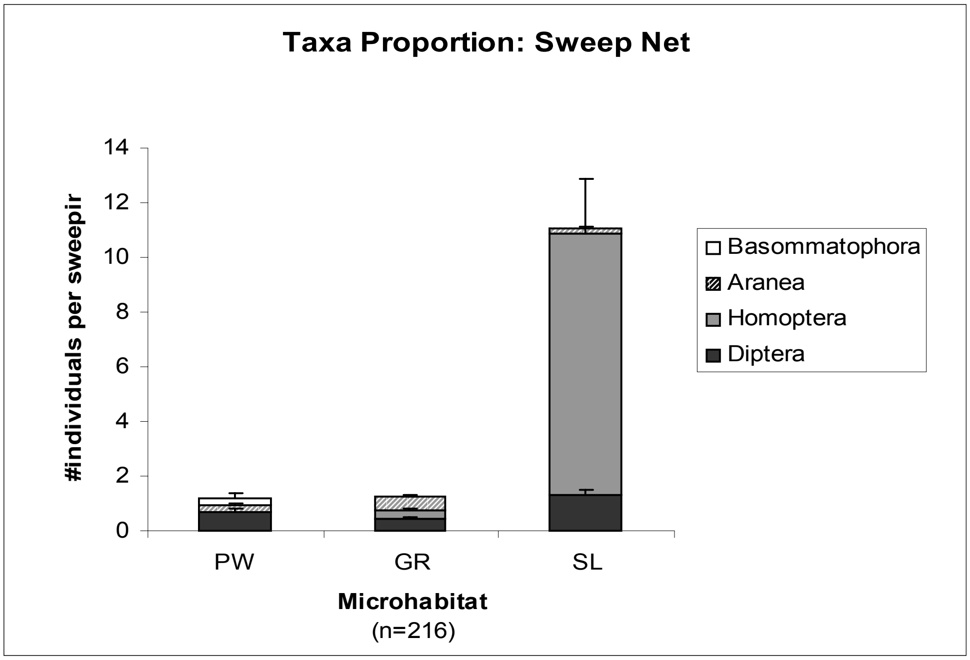

Figure 7. Proportions of total flying invertebrates (and snails) caught in sweep nets. The slough zone column is completely dominated by the numbers of Homoptera (the order to which *P. marginata*, the plant hopper belongs). Various Diptera families fill in most of the rest of the slough zone numbers, with spiders making a relatively small contribution in terms of individual numbers.

Snail quadrat data revealed significantly ($p < 0.001$) higher numbers of snails in the *Grindelia* zone than in the pickleweed, with an average of 7.60 snails per quadrat, compared with only 4.71 snails per quadrat in the pickleweed. No Basommatophera were found in the sloughs through this or either of the other methods used in the study.

Song Sparrow Diet Variety: Richness and Evenness of the Invertebrate Community Different field methods yielded different levels of diversity and richness, and showed both normal and non-normal distributions. The Kurtosis values for the Simpson Diversity Index at the order level for pickleweed, *Grindelia*, and slough zones were 0.284, 1.299, and 21.697, respectively, for pit trap; the same index and zones showed K values of -0.674, -1.292, and 0.638, respectively, for sweep netting. Order richness distributions for both methods in all three zones approached normal. Comparison of zones for each index and method yielded data which are summarized in Table 3.

	Index	Microhabitats			ANOVA	
		Pickleweed	*Grindelia*	Slough	F - ratio	P-Value
Pit Trap	N_O	1.304 ± 0.773	1.014 ± 0.853	0.563 ± 0.579	17.677	P<0.001
	λ^*	0.129 ± 0.182	0.110 ± 0.197	0.015 ± 0.075	n/a	P<0.001
Sweep Net	N_O	1.139 ± 1.052	1.194 ± 1.043	1.278 ± 0.892	0.353	P=0.703
	λ	0.175 ± 0.254	0.190 ± 0.254	0.129 ± 0.194	1.315	P=0.271

Table 3. F-ratios and p-values from ANOVA for two measures of three microhabitats via two different field methods. Sweep netting showed no difference between any of the zones in order richness or diversity according to Simpson's Diversity Index. Pit trapping, however, showed a significant difference between pickleweed and *Grindelia* zones versus the slough zone. N_O= Order Richness (total number of taxa present); λ= Simpson's Diversity Index (based on abundance and number of taxa). * Kruskal-Wallis analysis of variance was performed in place of ANOVA because the distribution of this row's data did not fit ANOVA's assumptions.

For both capture methods, pickleweed and *Grindelia* zones were very similar in both richness and evenness (diversity). All orders counted in the survey were present in both zones, except Orthoptera, which was only found in *Grindelia* but was caught too rarely to for confident comparison (only a single grasshopper was captured in over 400 pit trapping and sweep netting occasions). However, pit trapping showed a deviation of the slough from the values of the other two zones. Sweep netting did not reveal any differences in variety of prey items.

Discussion

Viable prey items for song sparrows in the tidal salt marsh have a zonation almost as discrete as the vegetation on which many of the invertebrates base their own food webs. The separation of orders along vegetation lines was expected, as many ecologists believe that patterns in food supply influence patterns in diversity (Mackay and Kalff 1969, Cameron 1972). The most unexpected finding was the relative lack of diversity in the slough zone, as emphasized by Table 3. Though the original hypothesis expected higher diversity because of habitat structure complexity, this particular surprise may be explained by the theory of intermediate levels of disturbance interference, suggested by Connell in 1978 (Bradbury 1995). The "Goldilocks" hypothesis asserts that a disturbance which interrupts a community enough to allow less competitive groups to be successful, while not being severe enough to cause local extinctions, will effect high diversity. If one were to base an hypothesis on this idea, one might come to the conclusion that in this system there would be the highest level of diversity and richness on the marsh plain, or in the pickleweed zone, because that is the area that receives the intermediate amount of tidal inundation, a major source of disturbance. The slough would have the lowest diversity based solely on this hypothesis because it is affected by the tide most frequently.

However, the theory doesn't completely explain the shared higher richness and diversity values of both the *Grindelia* and pickleweed zones. The height of the *Grindelia* bushes and the land beneath them may help to finish the concept; the broad range of the insects found in this zone probably allow for travel between the high bushes and the upland areas that are not affected by the same abiotic zoning factors that the salt marsh is subject to. In this case, the insects found in *Grindelia*, and in fact many of the flying insects in total, would not be constrained in the same way that invertebrates with a shorter traveling range would be. This functional view also offers an explanation for observed differences between methods. Pit trapping, which is more successful at capturing invertebrates that don't fly, would be more likely to show a difference in diversity or richness between the areas of land that are not frequently under water and the slough, which is often under water. One would expect to find more ground-traveling invertebrates on what may usually be considered relatively dry land than in the slough where a walking insect, for instance, would not be able to escape a quick tide.

How do these data relate to song sparrow feeding, and more importantly for the purposes of this study, song sparrow defense of territory? According to the basic optimality theory of foraging (Schoener 1971), birds will choose prey that is easy to catch, quick to handle, and nutritionally rewarding. In this system, the translation of these concepts is relatively straightforward: of the taxa surveyed, there are two main modes of transportation for the invertebrates: by ground or by air. For the sit-and-wait ambush style of foraging that the song sparrows employ (Nice 1937), invertebrates that move on the ground would take less energy to catch than those that fly. Ease of handling can be interpreted as having a protective shell. The only invertebrate sampled which might fit this category is *M. myosotis*, the small snail found in the *Grindelia* and pickleweed zones. The shell on the snail is very thin and may not pose a very large problem for the song sparrows, whereas the shell of a mussel or a clam might. If this statement is accurate, all invertebrates sampled in this study can be considered to be of approximately equal handling difficulty, with snails being slightly less desirable for this reason. Finally, energy reward may be thought of as biomass. In a study where adult birds were given a choice of prey that were equally difficult to catch and handle, the birds always chose the larger items as long as the prey was abundant (Krebs et al. 1977). The amphipod *T. traskiana* was by far the heaviest invertebrate, with *M. myosotis* as a distant but definite second (the snails weighed half as much as the amphipods, but were still considerably heavier than the next heaviest taxon, a fly; see Figure 3). By contrast, the other very abundant invertebrate sampled, *P. marginata,* is also the lightest. A song sparrow would need to catch and eat over 30 of these plant hoppers in order to get the same mass of food it would get if it ate a single amphipod. Additionally, during breeding season, large prey is in higher demand because birds typically feed their young even larger prey than they themselves generally eat (Davoren and Burger 1998).

As one of the two most abundant taxa, as well as being easy-capture and the heaviest invertebrate collected, *T. traskiana* is likely a very significant part of the song sparrow food base. Preliminary results from stable isotope work by Grenier (2002, pers. comm.) suggest that this is probably the case; the data show that song sparrows are at least sometimes eating amphipods, as well as snails.

Distributions suggest that prey quality (in terms of optimization) and especially abundance outweigh variety, as evidenced by the foraging preferred in pickleweed over *Grindelia*, which is within the defended territory, and was found to be just as diverse and rich in song sparrow food types. And while snails are more abundant in the *Grindelia* zone, the high abundance of amphipods and concurrent presence of a still high number of snails in the pickleweed may have prompted foraging in this zone. According to Gilliam and Fraser (1987), animals usually learn which areas are best for foraging and return there often. If this is the case, then the area to which song sparrows continue to return, the pickleweed, is the best area in which to forage.

Unfortunately, several theoretical and actual difficulties arose from the methods used in this study. A potential area of bias introduced by pit trapping is the water used at the bottom of the pit traps. The purpose of the water was to keep invertebrates from jumping out of the pit traps, but it is unclear whether it drew invertebrates into the traps. Another problem was with the nature of the different field methods, which essentially fragmented the data collected. Because the units of capture of the different methods could not be standardized (i.e. a number of individuals per unit time per area), data between the two methods cannot be directly compared. For example, it would not be possible to conclude which invertebrate, amphipod or plant hopper, has a higher absolute abundance in the salt marsh from this data.

Despite these drawbacks, the data of this study clearly suggest that the pickleweed represents an area of high biomass made up of invertebrates which are easy for song sparrows to catch and handle, while *Grindelia* represents an area of intermediate biomass and high variety of both flying insects and walking or crawling invertebrates, and the slough represents an area of high abundance but very low biomass. From these conclusions, one can reasonably infer that the extremely high abundance of energetically favorable food in the pickleweed reduces the need for protection of these resources from competitors. Because the energetic cost of defending an area is high (Van Tyne and Berger 1976), it behooves the song sparrows to defend smaller territories as long as their food resources are not limiting.

This major affect on bird territory structure by the simple distribution of tidal salt marsh invertebrates exemplifies how important invertebrates are to the community as a whole. Conservationists and planners of wetland enhancement or restoration projects would benefit greatly from thorough studies of invertebrate groups and their contributions to the communities of which they are a part. Having a better understanding of the complex relationships between this commonly overlooked group and the rest of its community is essential for making sound decisions about the future of habitats in the San Francisco Bay Area.

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