




Stable isotope mixing models demonstrate the role of an invasive plant in wetland songbird food webs

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Abstract

Premise: Invasive plants in wetlands are often ecosystem engineers, mediating changes in ecosystem functions like trophic support. We documented the impacts of *Lepidium latifolium*, an invasive plant, on the food web of omnivorous birds (Suisun song sparrows, *Melospiza melodia maxillaris*) in a tidal wetland of northern California, USA.

Methods: We used analysis of natural abundance stable isotopes of ¹³C and ¹⁵N in song sparrow blood, invertebrate food sources, *L. latifolium* seeds, and other marsh plant seeds to inform Bayesian, concentration-dependent mixing models that predicted average song sparrow diets.

Results: Season and plant phenology influenced food source incorporation and isotopic signatures. Song sparrows showed higher isotopic variability in the summer. The observed changes in song sparrow diets were driven by altered invertebrate communities related to seasonal *L. latifolium* presence and by shifts from seeds to consumption of invertebrate food sources during the breeding season in the spring and summer.

Discussion: This study used stable isotope tools and modeling to demonstrate two mechanisms of isotopic influence by *L. latifolium* on omnivorous song sparrows. This study can inform site- and species-specific management strategies by demonstrating how changes to the plant community can impact entire trophic systems.

KEYWORDS

invasion, *Lepidium*, mixing models, stable isotopes, tidal wetlands, trophic

Wetlands provide numerous ecosystem functions and services, including maintenance of biodiversity, habitat provision, trophic support, nutrient cycling, carbon sequestration, and water filtration (Mitsch and Gosselink, 2007). The presence of plants in wetlands affects these ecosystem-level processes (Marinelli and Waldbusser, 2005), and thus shifts in vegetation composition and species identity can cause large-scale ecosystem changes due to direct influence on ecosystem functions and induced changes in the distribution of other organisms (Eviner and Chapin, 2003).

Due to their position at the boundary of the terrestrial, freshwater, and marine systems, tidal wetlands often experience large-scale vegetation shifts through establishment of invasive plants (Zedler and Kercher, 2004). Acting as ecosystem engineers that exert indirect or direct control over resource availability (Jones et al., 1994), invasive species can fundamentally change ecosystems by impacting ecosystem services (e.g., Pejchar and Mooney, 2009; Funk et al., 2014), threatening endangered species (e.g., Dueñas et al., 2021), and altering food webs (e.g., David et al., 2017).

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Plant invasions stand to have more negative impacts on tidal wetland obligates, as opposed to upland, generalist bird species (Greenberg et al., 2006; Takekawa et al., 2006), making invasive plants a primary concern for managers and conservation scientists. However, predicting the effects of plant invasions on omnivorous foragers at large spatial scales remains difficult, and our ability to anticipate impacts on native biodiversity is still limited (Seabloom et al., 2006). Exploring novel applications of existing technologies in sensitive habitats is critical to understanding the role of invasive species and better managing affected ecosystems. In this study, we explore how an invasive plant alters the food web of an endemic, tidal wetland songbird by applying Bayesian, concentration-dependent mixing models to natural abundance stable isotope data.

Prior studies have explored the effects of invasive plants on tidal wetland invertebrates and food webs (e.g., Gratton and Denno, 2005 [*Phragmites australis*]; Levin et al., 2006 [hybrid *Spartina*]; Wigginton et al., 2014 [*Lepidium latifolium*]), but less research focuses on the food web impacts of invasive plants on higher trophic levels including omnivorous marsh vertebrates, like fish and birds. Isotopic studies have used species-specific discrimination factors and mixing models to show that invasive wetland plants are incorporated into the diets of fish, but these studies have primarily used basal food sources to understand plant impacts on higher trophic levels (Weinstein et al., 2010; Dibble and Meyerson, 2014). Studies that have focused on impacts to birds often document the use of invasive plants as structure for foraging or nesting substrate. There is concern that invasive plants may provide less suitable nesting habitat, causing nest flooding or increased interspecific competition (Benoit and Askins, 1999; Guntenspergen and Nordby, 2006; Nordby et al., 2009). Some studies (e.g., Kennedy and Hobbie, 2004; Levin et al., 2006; Takekawa et al., 2006; Gan et al., 2009) have proposed potential trophic impacts of invasive plants on tidal wetland birds, but these suggestions are based on changing invertebrate abundances, loss of structural foraging habitat, or declining bird abundance, not on direct diet or isotopic studies of insectivorous or omnivorous birds (Levin et al., 2006; Takekawa et al., 2006).

Direct isotopic quantification of the impacts of invasive plants on tidal wetland birds will advance our understanding of these potential trophic impacts and could be particularly useful in sensitive tidal wetlands. Stable isotope analysis integrates across time periods, minimizing disturbances from repeated sampling such as trampling of plants, compaction of sediment, or altered behavior of sensitive species (e.g., Zedler, 1982; Hamberg et al., 2010). Examining isotope integration in the diet over several months can help overcome the limitations of other sampling methods, like cameras, that are constrained by deployment duration. Despite these advantages, stable isotope analysis has rarely been used to explore how invasive plants are incorporated into the food webs of species that forage across multiple trophic levels, especially for cases involving endangered or special status wildlife populations. Thus, stable isotopes have

been widely used to track energy sources and pathways into and through aquatic food webs, but tracking how basal food sources support multi-level food webs is still a novel use of this tool, especially when the application solves challenging field conditions in sensitive habitats (e.g., Glibert et al., 2019).

We quantified the impacts of invasive *Lepidium latifolium* L. (Poaceae) on the diet of Suisun song sparrows, *Melospiza melodia maxillaris*, a California species of special concern (Spautz and Nur, 2008). By applying Bayesian, concentration-dependent mixing models to stable isotope data from Suisun song sparrow blood, invertebrate food sources, *L. latifolium* seeds, and other marsh plant seeds, we were able to examine the integration of *L. latifolium* into Suisun song sparrow diets. We hypothesized that *L. latifolium* was integrated into the diet of the Suisun song sparrow through direct consumption of *L. latifolium* seeds and through indirect consumption of invertebrates that fed on the invasive plant, but this trophic support from *L. latifolium* would vary according to the plant's phenology. This would concur with the findings of David et al. (2017), who suggested invasive species at the base of the food web can provide positive support for higher trophic levels.

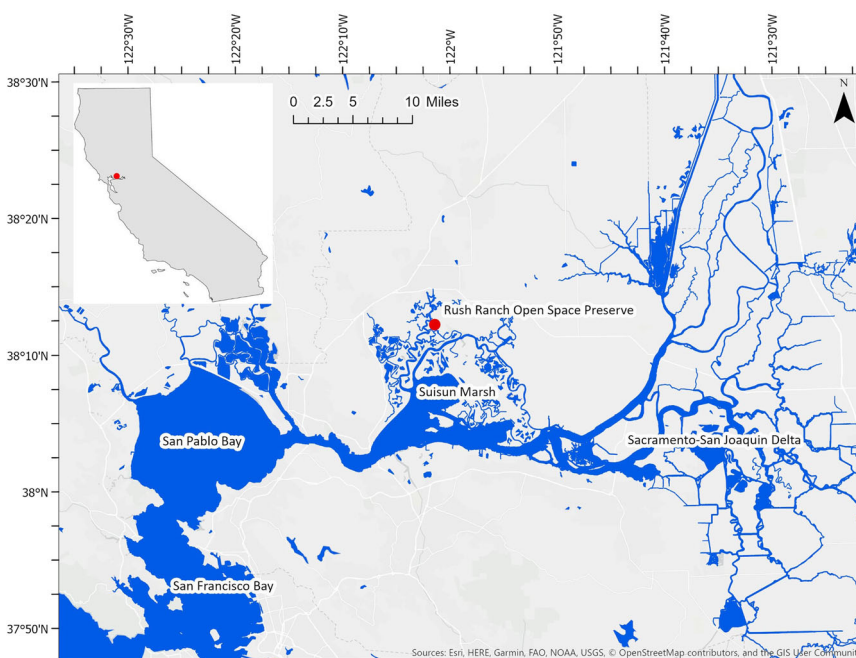
METHODS

Study site

Suisun Marsh is the largest brackish marsh ecosystem on the west coast of the United States (Moyle et al., 2014) and is transitional between the marine influence of the San Francisco Bay and the freshwater dynamics of the Sacramento–San Joaquin Delta (Figure 1). Suisun Marsh is dominated by diked wetlands managed for hydrology and plant assemblages that attract and support waterfowl (Arnold, 1996). Rush Ranch Open Space Preserve (Rush Ranch) protects a remnant historical tidal wetland along with its unique plant assemblage, including numerous rare and endemic species (Grewell et al., 2014). However, Whitcraft et al. (2011) estimated 27% of the flora at the site were non-native and noted that several invasive plants had established and proliferated in the modified hydrology and complex geomorphology at Rush Ranch (Fiedler et al., 2007; Whitcraft et al., 2011). One particularly aggressive invasive weed, *L. latifolium*, is a species of concern for land managers in Suisun Marsh and the broader San Francisco Bay–Delta Estuary.

Lepidium latifolium occurs naturally in Europe and the central and southwestern regions of Asia (Young et al., 1995) and is a widespread invader of the continental United States. Along the northwest coast of the United States, *L. latifolium* invades rangelands, riparian areas, and wetlands (Young et al., 1997; Leininger and Foin, 2009), outcompeting native grasses, sedges, and rushes (Blank and Young, 2002). Within the San Francisco Estuary, *L. latifolium* occurs in tidal wetlands across a salinity gradient from brackish to fully saline (Leininger and Foin, 2009). Most specifically, in the

FIGURE 1 The study site at the Rush Ranch Open Space Preserve shown in the context of the entire Suisun Marsh and Sacramento–San Joaquin Delta ecosystem.



brackish marsh at Rush Ranch, *L. latifolium* is known to decrease biomass of native plants (Whitcraft, unpublished data), increase invertebrate abundance in the spring through the summer, decrease invertebrate abundance in the winter, and seasonally increase canopy height and complexity relative to the native plant community (Wigginton et al., 2014).

Rush Ranch is home to a diverse avifauna including the Suisun song sparrow (*Melospiza melodia maxillaris*, hereafter song sparrow), a California species of special concern (Spautz and Nur, 2008). The loss of tidal wetlands has likely been a factor in the declining song sparrow populations in Suisun Marsh and the western Delta from an estimated ~300,000 birds in the 1800s (Grinnell and Miller, 1944; Spautz et al., 2005) to ~50,000 today (Shuford and Gardali, 2008). Song sparrows feed omnivorously on seeds and arthropods found in or below the plant canopy and build their nests in the brackish marsh vegetation (Brush et al., 1986; Grenier and Greenberg, 2006; Takekawa et al., 2011; Spautz et al., 2012). Territories of song sparrows range in size from the theoretical maximum observed in intact marshes of 30×153.6 ft (9.1×46.8 m) (Collins and Resh, 1985; Marshall and Dedrick, 1994; Spautz et al., 2005) to much smaller territories in fragmented marshes. Typically, song sparrows at Rush Ranch forage very close to their nests during the breeding season in the spring and the summer and hold more diffuse territories after their last clutch has fledged in the fall (Marshall, 1948) or late summer (Spautz et al., 2005). Due to its reliance on brackish marsh during all parts of its life history (Marshall, 1948; Marshall and Dedrick, 1994), the Suisun song sparrow is an excellent vertebrate study species for examining the multi-trophic impacts of an invasive wetland plant.

Experimental design

We randomly selected a zone in the brackish marsh at Rush Ranch where *L. latifolium* co-occurred with song sparrows. Our study area was adjacent to a primary tidal channel (Suisun Slough) and bounded by upland habitat on the east and second-order tidal channels on the north, south, and west. The study area contained the three major habitat types found in the brackish marsh at Rush Ranch, which are characterized by geomorphology, vegetation community, and distance from the creek. Fringing brackish marsh areas are immediately adjacent to unvegetated, subtidal channels and characterized by tall emergent vegetation; brackish marsh plains are drained areas of higher elevation crossed in numerous places by small tidal creeks and are dominated by lower-statured herbs and shrubs; brackish marsh–terrestrial ecotones are areas of marsh directly adjacent to surrounding upland ecosystems with a mixture of marsh and upland plants (Whitcraft et al., 2011).

We sampled bird blood prior to *L. latifolium* emergence (February–March 2011, hereafter “Winter,” $N = 17$ birds) and during *L. latifolium* bloom (July–August 2011, hereafter “Summer,” $N = 11$ birds). We generated a series of random points within the study zone, and the three nearest sparrow territories and their associated breeding pairs were targeted with mist nets (6–12 m in length). Once three pairs were captured or a reasonable effort had been made (2–3 h), we moved to the next random point (Figure 2 shows locations of nets where individuals were captured). The sample size is uneven due to inclement weather, which delayed summer sampling. Blood samples (20–40 μ L) were taken by brachial venipuncture and immediately put on ice in the field. The samples were frozen upon return to the laboratory and processed within 10 days as described below. All bird

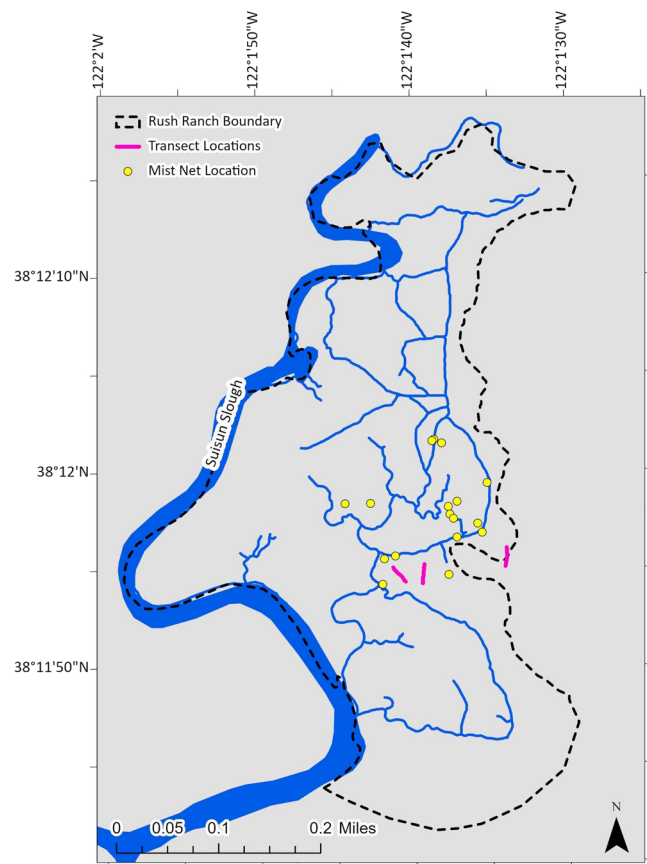


FIGURE 2 Detailed view of the study site at the Rush Ranch Open Space Preserve with transect and mist net locations shown. Map data: Google (Menlo Park, California, USA), Maxar Technologies (Westminster, Colorado, USA).

handling and processing was done in accordance with our agreement with the California State University Long Beach Institutional Animal Care and Use Committee (IACUC #284) and the Federal Bird Banding Lab (Permit #23446).

To pair these consumer samples with isotopic sources, we randomly selected a subzone in our study area bounded by second-order tidal channels. We delineated paired transects, separated by no more than 10 m, in each of the three habitat types (fringing brackish marsh, brackish marsh plain, and brackish marsh–terrestrial ecotone). One of the pairs was in a *L. latifolium*-invaded area (hereafter “invaded”), and the other was in a community containing no *L. latifolium* (hereafter “uninvaded”; Figure 2 shows paired transect locations). Invertebrate samples were taken along the transects ($N=6$; $N=3$ invaded and $N=3$ uninvaded) in both Winter (February 2011) and Summer (August 2011). Canopy-dwelling invertebrates were sampled using a leaf blower modified to take in air. Invertebrates were vacuumed from the plant canopy for 30 s per sample, gathered in cloth netting, and frozen at -20°C in the laboratory. Ground-dwelling invertebrates were sampled by taking non-quantitative scoops of the top 6 cm of soil to capture both epifauna and infauna. Soil scoops were rinsed on a

300- μm sieve and sorted live. Following identification, all ground-dwelling invertebrates were kept alive in brackish water and allowed to evacuate their guts for up to 24 h. Both canopy-dwelling and ground-dwelling invertebrates were identified to the family level or lower. Seed samples were taken opportunistically from the vacuum samples taken for canopy-dwelling invertebrate samples in Winter. Details of the specific organisms captured in this sampling are provided in Wigginton et al. (2014).

In preparation for stable isotope analysis, invertebrates and seeds were washed in Milli-Q water (Millipore, Billerica, Massachusetts, USA) to remove any outside contaminants and were dried at 65°C in tin boats. After drying, the seed samples were ground into a homogenous powder. Song sparrow blood was treated as whole blood, dried in a freeze dryer for 12 h, and stored in a desiccator until analysis. Stable isotope samples were analyzed at the University of California Davis following the protocol described by Whitcraft and Levin (2007). Mass spectrometry in conjunction with an elemental analyzer (PDZ Europa ANCA-GS; PDZ Europa, Northwich, United Kingdom) was employed to determine the isotopic composition of consumer and food source samples. Stable isotope abundance is expressed in parts per thousand (‰) in a ratio of heavy to light isotope content ($^{15}\text{N} : ^{14}\text{N}$ or $^{13}\text{C} : ^{12}\text{C}$). Vienna Pee Dee Belemnite was used as the carbon standard, and nitrogen gas was used as the nitrogen standard. Typical sample standard deviation was 0.2‰ for ^{13}C and 0.3‰ for ^{15}N (<https://stableisotopefacility.ucdavis.edu/carbon-and-nitrogen-solids>).

Statistical approach

We used permutational analysis of variance (PERMANOVA) in PRIMER 7 software (PRIMER-e, Auckland, New Zealand) to examine differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bird blood, invertebrates, and seeds between the Winter and Summer seasons. Euclidean distances were applied to create a matrix of similarity for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and PERMANOVA was applied to these matrices. There were 1–21 (average 6.31) replicates of each food source per season, although not every food source was replicated in both seasons. Bayesian mixing models, via the simmr package in R (Parnell, 2019), were used to estimate relative contributions of seed and invertebrate sources assimilated by song sparrows across the Winter and Summer seasons (following Parnell et al., 2013). Bayesian mixing models generate statistical distributions of isotopic values to address the inherent variability in food sources and in consumers (including trophic discrimination factors) to estimate food source contributions to an organism's or a population's diet (Parnell et al., 2013; Phillips et al., 2014). Estimations of source contributions can be dependent on the geometric proximity and relationship of the consumer relative to the sources in the mixing model space as well as statistical distinctions among sources (Phillips et al., 2014). Separate mixing models were run for each season using available and

likely food sources, including canopy-dwelling invertebrates, ground-dwelling invertebrates, *L. latifolium* seeds, and seeds from other marsh vegetation (primarily chenopods). Because the exact proportional incorporation of these food sources in song sparrow diets is not well understood and sometimes based on observational data, the Bayesian priors assumed an equal probability of each food source being consumed to avoid biased statistical inference (e.g., Northrup and Gerber, 2018). In addition, fractionation factors for Suisun song sparrows are unknown, and were therefore estimated to be 2.43 ± 0.48 for $\delta^{15}\text{N}$ and 0.43 ± 1.36 for $\delta^{13}\text{C}$ using the SIDER package in R (Pearson et al., 2003; Healy et al., 2018). Concentration-dependent (Phillips and Koch, 2002) mixing models correct for over- or underestimation of the source mass contributions to the mixture (song sparrow blood) by accounting for differences in elemental concentrations among sources (invertebrates and seeds).

RESULTS

Food sources

Invertebrate taxonomic orders were grouped through statistical and biological reasoning (Gannes et al., 1998; Phillips et al., 2014). Isotopic signatures of invertebrate food sources differed in pairwise analyses by order and season (Table 1, Appendix S1), with differences driven by low $\delta^{15}\text{N}$ values in gastropods in Winter (*Pseudosuccinea columella*; Table 2, Appendix S2). Because gastropods are isotopically distinct, they were grouped individually as a food source for the mixing model (Gannes et al., 1998), while other invertebrate sources were grouped as canopy- and ground-dwelling invertebrates based on our previous work on *L. latifolium*'s impacts on invertebrates (Wigginton et al., 2014) and our natural history observations of song sparrow foraging habits. Isotope sample sizes and taxonomic order within these groupings can be found in

TABLE 1 Comparison of pairwise PERMANOVA results of invertebrate carbon and nitrogen signatures between Winter and Summer, for each food source (grouped by higher taxonomic groupings).

Food source	PERMANOVA results		
	<i>t</i>	<i>P</i> (perm)	<i>P</i> (MC)
Coleoptera	1.0894	0.346	0.307
Diptera	1.1092	0.301	0.291
Oligochaeta	1.8243	0.065	0.07*
Amphipoda	2.4978	0.008	0.008*
Gastropoda	1.7139	0.058	0.134
Araneae	0.71512	0.721	0.569

Abbreviations: *t*, test statistic from PERMANOVA tests; *P*(perm), level of significance for PERMANOVA tests; *P*(MC), level of marginal significance for Monte-Carlo PERMANOVA tests.

*Denotes significant comparisons.

Table 3. After classifying invertebrates in this way, mean isotopic signatures of the gastropods differed from the ground-dwelling invertebrates and canopy-dwelling invertebrates in Winter, while all invertebrate source types were similar in Summer (Appendix S3, Figure 3). We opportunistically collected seeds from our invertebrate samples and had no way to visually assess seed age and associated impacts of season; however, *L. latifolium* differed from other plant seeds in our samples in mean nitrogen signatures (Appendix S2). Seed values remained the same in both Winter and Summer (Figure 3), demonstrating our assumption that our opportunistic sample was an integration of the signatures of seeds across the seasons and that seeds were available to birds throughout the year.

TABLE 2 Source sample size and statistics for carbon and nitrogen signatures.

Source type	<i>n</i>	Mean C \pm SD	Mean N \pm SD
Canopy invertebrates	35	-25.27 ± 1.29	10.79 ± 2.4
Gastropoda	6	-25.16 ± 0.6	7.59 ± 0.72
Ground invertebrates	53	-24.87 ± 0.99	9.86 ± 1.35
<i>L. latifolium</i> seed	12	-24.77 ± 0.39	9.98 ± 0.71
Other seed	20	-27.72 ± 1.11	9.07 ± 1.81

TABLE 3 Abundance of food sources by season, source type, and order.

Season	Source type	Taxonomic grouping	<i>N</i>
Winter	Ground invertebrates	Amphipoda	13
		Oligochaeta	14
	Canopy invertebrates	Araneae	3
		Coleoptera	9
		Diptera	9
Summer	Ground invertebrates	Microcoryphia	1
		Amphipoda	21
		Gastropoda	2
		Isopoda	4
	Canopy invertebrates	Oligochaeta	1
		Araneae	3
		Coleoptera	4
All	Seeds	Diptera	4
		Hemiptera	2
		<i>L. latifolium</i>	12
		Caryophyllales ^a	19
		Poales ^b	1

^aPredominantly *Salicornia pacifica* and *Atriplex prostrata*.

^bPredominantly *Juncus balticus*.

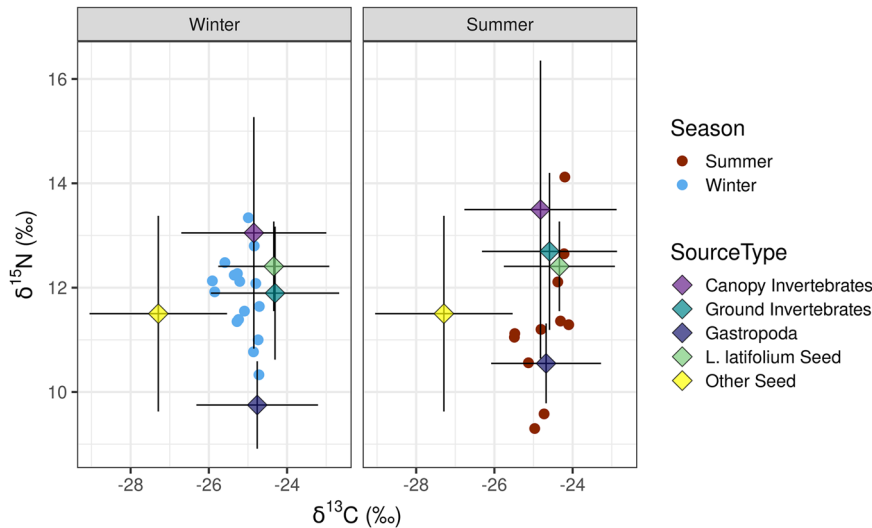


FIGURE 3 Dual isotope plot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (corrected with fractionation factors) of Suisun song sparrow blood divided by season (Winter and Summer) and categorized food source types as sampled in 2008 in the Rush Ranch Open Space Preserve.

TABLE 4 Source posterior distribution estimates.

Season	Source	Proportion (Bayesian credible interval)	Proportion (median)	Proportion (mean \pm SD)
Winter	Canopy invertebrate	{0.043, 0.335}	0.177	0.179 \pm 0.075
	Gastropoda	{0.04, 0.274}	0.142	0.146 \pm 0.06
	Ground invertebrate	{0.045, 0.441}	0.214	0.221 \pm 0.105
	<i>L. latifolium</i> seed	{0.058, 0.494}	0.253	0.259 \pm 0.113
	Other seed	{0.072, 0.322}	0.194	0.194 \pm 0.159
Summer	Canopy invertebrate	{0.02, 0.329}	0.113	0.130 \pm 0.083
	Gastropoda	{0.11, 0.654}	0.384	0.384 \pm 0.139
	Ground invertebrate	{0.021, 0.404}	0.143	0.161 \pm 0.104
	<i>L. latifolium</i> seed	{0.032, 0.521}	0.210	0.229 \pm 0.132
	Other seed	{0.019, 0.22}	0.088	0.096 \pm 0.053

Consumers

We sampled the blood of 17 birds during the Winter months prior to *L. latifolium* emergence and 11 birds in the Summer months during *L. latifolium* bloom. Mean isotopic signatures of the consumers differed by season (PERMANOVA, Pseudo $F_{[1,26]} = 3.16$, $P(\text{MC}) = 0.06$), which was likely driven by significantly heavier $\delta^{13}\text{C}$ values in Winter ($-25.15 \pm 0.1 \delta^{13}\text{C}$) as opposed to Summer ($-24.71 \pm 0.15 \delta^{13}\text{C}$) in song sparrow blood (Pseudo $F_{[1,26]} = 7.65$, $P(\text{MC}) = 0.01$).

Mixing model

The *simmr* mixing model was used to estimate the possible contributions of food sources to the consumers' diets (Parnell, 2019). The model was separated by season to account for seasonal isotopic shifts, and food sources were classified into groups through statistical and biological reasoning as described

above in "Food Sources." The estimated proportion of each source within the consumer diet is represented as the range of 95% Bayesian credible intervals, median, and mean \pm SD (Table 4). The incorporation of other seeds decreased slightly between Winter (7.2–32.2%) and Summer (2–22%), while *L. latifolium* seed provided similar diet contributions between Winter (5.8–49.4%) and Summer (3.2–52.1%). Incorporation of ground-dwelling invertebrates and canopy-dwelling invertebrates was similar between Winter (ground 4.5–44.1%, canopy 4.3–33.5%) and Summer (ground 2.1–40.4%, canopy 2–32.9%). Finally, the incorporation of gastropods was lower in the Winter (4–27.4%); their proportion in the consumer diet increased in Summer to 11–65.4%. On average, our models predict Winter bird diets were $17.9 \pm 7.5\%$ canopy-dwelling invertebrates, $14.6 \pm 6\%$ gastropods, $22.1 \pm 10.5\%$ ground-dwelling invertebrates, $25.9\% \pm 11.3\%$ *L. latifolium* seeds, and $19.4 \pm 15.9\%$ other seeds (Figure 4). In Summer, average bird diets were predicted to be $13 \pm 8.3\%$ canopy-dwelling invertebrates, $38.4 \pm 13.9\%$ gastropods, $16.1 \pm 10.4\%$ ground-dwelling

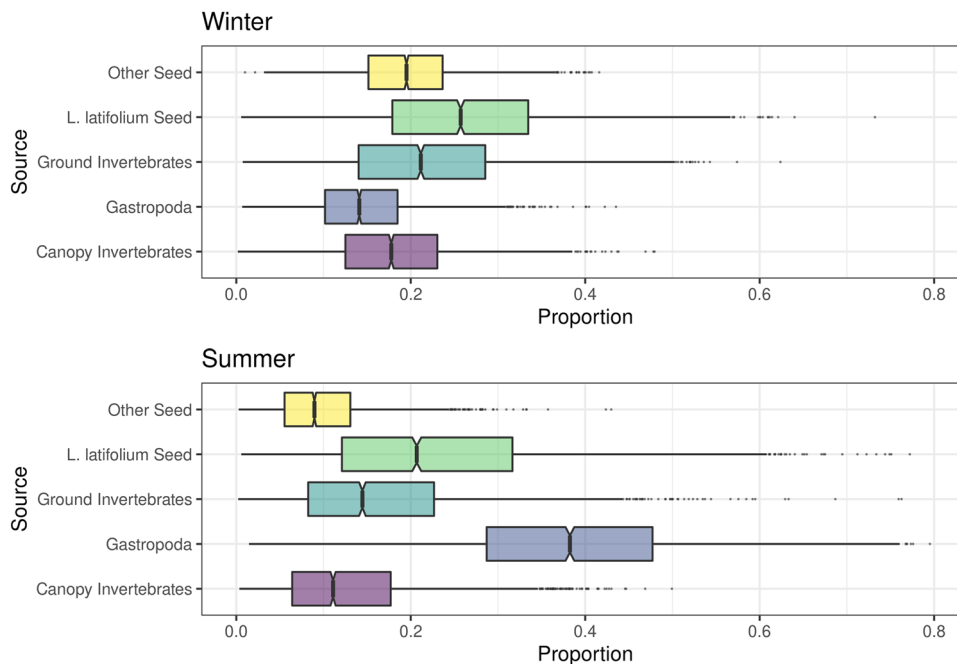


FIGURE 4 Contribution of different food source types to the diet of Suisun song sparrows estimated using Bayesian isotopic mixing models by season (Winter and Summer). Results show posterior model estimates (median, interquartile range, and maximum/minimum values) of source contribution to song sparrow blood.

invertebrates, $22.9 \pm 13.2\%$ *L. latifolium* seed, and $9.6 \pm 5.3\%$ other seeds (Figure 4).

DISCUSSION

Our stable isotope mixing models demonstrate direct consumption of invasive *L. latifolium* seeds by song sparrows and a seasonally shifting reliance on invertebrate food sources. First, we found that *L. latifolium* seeds constituted more than 20% of the average song sparrow diet across both Winter and Summer. This relationship suggests an invasive species at the base of the food web is directly providing caloric support for higher trophic levels (David et al., 2017), which has also been documented in wetland fish (Weinstein et al., 2010; Dibble and Meyerson, 2014). This seasonally consistent *L. latifolium* seed consumption contrasted with consumption of other seeds, which decreased in song sparrow diets between Winter (~19%) and Summer (~10%). Seed rain in tidal wetlands is structured by the total cover of plant species, volume of seed production, and seed characteristics for dispersal via tides (Diggory and Parker, 2011). In tidal wetlands of the San Francisco Estuary, seed production is assumed to begin in June and continue until January, with tidal action removing 20–90% of seeds from the system (Diggory and Parker, 2011). Thus, song sparrows, which predominantly feed on seeds that have dropped to the marsh sediment surface (Marshall, 1948; Takekawa et al., 2011), likely experience the highest seed availability in late summer

through early fall after seeds have ripened and begun to drop to the marsh surface. However, *L. latifolium* seeds may be more consistently available across the year due to the plant's truly prolific seed production, documented as high as 1,600,000 seeds/m² (Young et al., 1997). Our models mirror this seed availability and show that seeds from other marsh plants are consumed more in Winter at the end of peak availability of seeds, whereas *L. latifolium* seeds are consumed year-round. Additionally, in the brackish marsh–terrestrial ecotone at Rush Ranch, *L. latifolium* invasion decreased *Salicornia pacifica* Standl. cover (Whitcraft, unpublished data), which was the other predominant seed type in our isotopic samples. In conclusion, not only do song sparrows eat *L. latifolium* seeds readily, but the invasive plant is also potentially decreasing the availability of other seeds by shifting plant community composition.

In addition to this seasonal shift in seed consumption, we found average song sparrow diets consisted of approximately 40% invertebrate food sources in Winter and over 65% invertebrate food sources in Summer. A similar shift from seeds to invertebrate food sources between the winter and the summer has been documented in closely related tidal wetland song sparrows (*Melospiza melodia samuelis*) and corresponds with the summer breeding season when nutritional needs are higher (Grenier, 2004; Grenier and Greenberg, 2006). In addition, these related sparrows consumed more marine invertebrates than insects (Grenier, 2004; Grenier and Greenberg, 2006). Our findings are similar, with gastropods as a dominant food source in song sparrow diets in the

summer breeding season. Although the source contribution between ground-dwelling invertebrates and *L. latifolium* seeds should be interpreted carefully due to their statistical and geometric similarity, ground-dwelling invertebrates (mainly marine taxa, Table 3) predominate diets in the Winter, while canopy-dwelling invertebrates (mostly insects and spiders, Table 3) accounted for a similar, smaller proportion of the average song sparrow diet across seasons (approximately 15.5%).

The gastropod species in our samples, *Pseudosuccinea columella* (Lymnaeidae), is invasive (Ray, 2005). Previous observations of Lymnaeidae in Suisun Marsh in the diet of invasive white catfish (as Lymnaeidae; O'Rear, 2007) are very likely also *P. columella*. Our models demonstrated that gastropods were consumed much more heavily in Summer than Winter, which could reflect the dominant seasonal patterns in abundance of benthic invertebrates in the San Francisco Estuary (Howe et al., 2014; Whitley and Bollens, 2014), a preference for invertebrates in the summer breeding season, or both. In addition to this seasonal variation in benthic invertebrate composition, invertebrate community shifts can be driven by the associated vegetation community (Howe et al., 2014). Specifically, the presence of *L. latifolium* has been shown in prior studies to increase ground-dwelling invertebrate abundance in the brackish marsh–terrestrial ecotone (Wigginton et al., 2014). The mechanisms behind these differences are still unclear but could be related to changes in light regime where *L. latifolium* has been measured as both increasing (Whitcraft, unpublished data; Wigginton et al., 2014) and decreasing shading (Reynolds and Boyer, 2010). This suggests *L. latifolium* may be locally increasing food availability on the ground surface, at least in parts of the marsh. Soft-shelled gastropods, such as *P. columella*, may have been underestimated in previous diet studies because they are difficult to identify in analyses of gut contents, and observational studies of feeding dynamics at the sediment surface are challenging because of thick brackish marsh plant cover.

Less is known about the terrestrial invertebrates living in the plant canopy of Suisun Marsh (Moyle et al., 2014). Previous studies have shown *L. latifolium* altered insect and spider community composition in the canopy relative to non-*L. latifolium* areas (Reynolds and Boyer, 2010), seasonally increased canopy-dwelling invertebrates in the summer, and depressed canopy-dwelling invertebrate abundances during plant senescence in the winter (Wigginton et al., 2014). Despite a seasonal decrease in abundance of invertebrates and the local decrease mediated by *L. latifolium* senescence (our previous study sampled concurrently to Winter blood samples), our models showed canopy-dwelling invertebrates occupied a similar proportion in song sparrow diets across both seasons. A greater year-round reliance on seed as opposed to invertebrate food sources (both ground- and canopy-dwelling) in Suisun song sparrows supports prior evolutionary work on tidal marsh song sparrow subspecies of the San Francisco Estuary (Grenier and Greenberg, 2005). Differences among these subspecies are characterized by

coloration as well as bill shape and size. The longer, thinner bills of *Melospiza melodia samuelis* and *M. m. pusillula* were proposed to be adaptive for closing quickly and reaching into crevices in the marsh sediments to capture invertebrate prey (Grenier and Greenberg, 2005). Suisun song sparrows are called *M. m. maxillaris* because their bills are stouter and shorter than its two sister species, and historical treatments of Suisun song sparrow diets reported birds relied heavily on seeds (predominantly *Typha* L. and *S. pacifica*; Marshall, 1948). Although *Typha* seeds are not well-represented in our samples, our isotopic results suggest Suisun song sparrows, which breed in brackish marsh, may rely more on plant foods year-round than the other two subspecies of song sparrows, which breed in salt marshes, illustrating key differences in the needs of these subspecies of special concern.

With data from our diet models, we hypothesize that these seasonal isotopic patterns are the outcome of intra-annual changes in food availability, changes in energetic needs during the breeding season, and the impacts of *L. latifolium* invasion on food sources. Isotopes have been used in studies of seaside sparrows (*Ammospiza maritima*) in Louisiana, USA, to show diet flexibility in response to large-scale stressors such as oil spills or hurricanes (Olin et al., 2017; Moyo et al., 2021), but, to the best of our knowledge, no similar studies have used stable isotopes to quantify diet impacts of an invasive plant on tidal wetland birds. Our approach uses analysis of bulk stable isotopes with modeling techniques to advance previous studies of Suisun song sparrow natural history and known impacts of *L. latifolium* on food resources. Kimball et al. (2021) highlight compound-specific stable isotope analysis as a novel tool to trace energy flows from the base of the food web, and this approach has also been used to examine the contribution of carbon from two different source pools into the closely related seaside sparrows through invertebrate consumption (Johnson et al., 2019). We believe this is a strong approach for understanding the impacts of invasive plants across trophic levels and would allow future studies to trace *L. latifolium*-derived isotopes directly through the food web.

The impacts of invasive plants on ecosystems are particularly important to understand because of the outsized effects invaders can have (e.g., McDowell and Byers, 2019) and the extensive costs of controlling invader populations long-term (Crystal-Ornelas et al., 2021). Our results using stable isotope tools indicate invasive *L. latifolium* has been incorporated into Suisun song sparrow diets. When choosing invasive plant control or management actions, knowing the extent to which invasive plants have integrated into natural systems can help us avoid unintended negative consequences of invasive control actions that remove either structure or trophic support from associated organisms of concern (Neira et al., 2005; Lampert et al., 2014). For example, *L. latifolium* control may need to be paired with native plant restoration to provide adequate trophic support to song sparrows. Advanced tools, such as stable isotope analysis and

concentration-dependent mixing models, can be used to accurately assess trophic impacts of invasive plants, to inform invasive plant control, and to prioritize restoration efforts in dynamic and delicate tidal marsh systems.

AUTHOR CONTRIBUTIONS

R.D.W., C.R.W., and H.S. planned and designed the research while R.D.W. and C.R.W. acquired funding to support the research. R.D.W. and C.V.G. curated the data, and C.R.W., R.D.W., and C.V.G. conducted the formal analysis of the data. All authors wrote and edited the first draft of the manuscript. All authors approved the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

Isotope (^{13}C , ^{15}N on sources and birds) data and R code for diet composition in Rmarkdown are available for download at <https://doi.org/10.5281/zenodo.6537819> (Wigginton et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Pairwise PERMANOVA results of invertebrate carbon and nitrogen signatures by order.

Appendix S2. Pairwise permutational ANOVA of carbon and nitrogen signatures among source type within season.

Appendix S3. Pairwise PERMANOVA results of source isotopic signatures by source type within season.

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