

# Habitat use is linked to resource-specific performance of an ecologically important marsh predator

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**Abstract.** It is commonly assumed that animals should preferentially use habitats that enhance their individual performance. However, there have been few attempts to empirically test the relationship between an animals' habitat use and performance. This is surprising, since knowing about this connection should enhance our ability to predict the local population dynamics of ecologically important species. Here, we used three primary experiments to assess the relationship between habitat use and performance for an important insect consumer (ladybeetles). First, we used field manipulations of resource availability (i.e., scale insects and cordgrass pollen) to examine the habitat use of ladybeetle predators. Second, we conducted a series of no-choice laboratory assays to compare the performance (fecundity and longevity) of ladybeetles on these different resources. Third, we quantified adult ladybeetle preference for olfactory cues from cordgrass with and without scale insects using a Y-tube olfactometer. In the field, adult ladybeetles selectively used plots containing scale insects. In the laboratory, diets containing scale insects maximized both adult and larval ladybeetle longevity, and adult fecundity. Adult ladybeetles were attracted to chemical cues associated with scale insects over distances of 10s of centimeters. Overall, our findings suggest that the habitat use and performance of ladybeetles are strongly linked, with ladybeetles preferentially using habitats that maximize their individual performance.

**Key words:** fitness; habitat cues; habitat selection; habitat–performance relationships; predation risk; resource identity; salt marsh.

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## INTRODUCTION

Understanding the drivers of habitat selection and use by animals has been a major theme in ecology. However, most studies of habitat use have failed to mechanistically test the relationship between habitat use and how resources in that habitat affect an individual's performance (e.g., fecundity and longevity). This is surprising, given that (1) habitats vary in resource quantity and quality and (2) resource quantity and quality influence the performance of individuals (Coll and Guershon 2002, McLoughlin 2007, Beyer

et al. 2010, Gaillard et al. 2010). Knowing how habitat-specific resources affect the performance and habitat use of ecologically important consumers will provide insights into which habitat factors (e.g., resource identity and availability) best predict local population dynamics.

Animals should preferentially use habitats with resources that enhance their individual performance and fitness (Hilden 1965, Van Horne 1983, Hutto 1985, Weins 1989, Rosenzweig 1991, Morrison 2001, Morris 2003). For example, herbivorous insects have greater reproductive performance when fed preferred plant types (Gripenberg et al.

2010). Yet, animals sometimes preferentially use seemingly poor-quality habitats. Such habitats may be utilized for several reasons. First, habitat use may be determined by factors outside of individual performance—based only on resource quality. Such factors include mate choice (Kokko and Sutherland 2001), site fidelity (Pulliam and Danielson 1991), and safety from predators (Lima and Dill 1990, Heithaus and Dill 2002). Similarly, animals may selectively use habitats with resources that maximize performance during more stressful environmental conditions not considered during the study period (Van Horne 1983). Second, organisms may select low-quality habitats if they have imperfect knowledge of their environment (Lima and Zollner 1996, Arlt and Pärt 2007). Imperfect knowledge can result from limited availability of environmental cues from high-quality habitats or mismatches between environmental cues and habitat quality (Orians and Wittenberger 1991, Schlaepfer et al. 2002). These observations suggest that habitat use may not always be determined by how resource quality within a habitat influences individual performance and targeted studies are needed to predict the habitat–performance relationships of ecologically important consumers.

In southern California salt marshes, the ladybeetle (*Naemia seriata*) stabilizes salt marsh communities by suppressing populations of pest insects and indirectly enhancing *Spartina foliosa* (hereafter, cordgrass) rhizome biomass (Rinehart et al. 2017). By enhancing cordgrass rhizome growth, ladybeetles may facilitate important marsh ecosystem functions including sediment stability and accretion (Pillay et al. 2011). Furthermore, ladybeetles are omnivorous and will often consume cordgrass pollen when it becomes available (S. A. Rinehart, unpublished data). Ladybeetles may consume pollen to complement their insect-based diet, as pollen is often an excellent source of carbohydrates and protein (Coll and Guershon 2002, Lundgren 2009). Thus, understanding how these two distinct resources (scale insects and cordgrass pollen) influence ladybeetle habitat use and performance will enable managers to better identify which salt marsh habitats are critical for ladybeetle persistence.

We assessed the relationship between habitat use and individual performance for an ecologically important ladybeetle consumer. Our model system included the two primary prey resources

for this ladybeetle, scale insects, and cordgrass pollen (S. A. Rinehart, unpublished data). We used this model salt marsh system to test how (1) resource availability influences ladybeetle habitat use under field conditions and (2) resource identity influences ladybeetle performance. More specifically, we examined how scale insect and cordgrass pollen manipulations impacted ladybeetle densities in the field. Then, we used a series of laboratory assays to assess how the presence and absence of scale insects and cordgrass pollen resources impact individual ladybeetle performance. Additionally, we examined the attractiveness of olfactory cues from these resources using a Y-tube olfactometer to understand the role of these cues in habitat selection.

## MATERIALS AND METHODS

### Study system

We assessed the relationship between habitat use and individual performance in the ladybeetle, *Naemia seriata*. We used ladybeetles as a model consumer for three reasons. First, ladybeetles consume two distinct food resources. Ladybeetles primarily consume scale insects (*Haliaspis spartinae*) but will also consume pollen from cordgrass (*Spartina foliosa*) when available (S. A. Rinehart, personal observation). Although ladybeetles may feed on other prey resources (e.g., planthoppers), they likely constitute only a small portion of ladybeetle diets, as alternative prey resources are less abundant than scale insects. For example, in areas of high ladybeetle abundance, scale insect density was  $16,177 \pm 2174$  per  $0.25 \text{ m}^2$  (mean  $\pm$  standard error [SE]), while planthopper density was only  $25 \pm 2.8$  per  $0.25 \text{ m}^2$  (mean  $\pm$  SE; S. A. Rinehart, unpublished data). Second, ladybeetle population dynamics are tied to the availability of scale insects (S. A. Rinehart, unpublished data). Third, ladybeetles likely make frequent decisions regarding habitat use because they are active predators that constantly moving on, and between, cordgrass stems while foraging (Rinehart et al. 2017).

### Effects of resource availability on ladybeetle habitat use

To understand how prey resources (i.e., scale insects and cordgrass pollen) impact adult ladybeetle habitat use, we conducted a manipulative

study in San Dieguito Lagoon (32°58'40.4" N, 117°14'32.8" W, hereafter SDL). On 29 August 2015, we established 32, 0.25-m<sup>2</sup> circular plots (separated by at least 1 m) in a monospecific cordgrass stand infested with scale insects. All plots started with at least four flowering cordgrass stems and had a stem density of  $12.7 \pm 0.4$  stems per 0.25 m<sup>2</sup> (mean  $\pm$  SE). In each plot, we manipulated scale insects (present/absent) and pollen access (present/absent) in a 2  $\times$  2 fully factorial design ( $n = 8$ ). In scale insect absent plots, we removed all scale insects on cordgrass stems using a soft toothbrush (Long and Porturas 2014, Rinehart et al. 2017). In scale insect present plots, we did not alter scale insect populations on cordgrass stems. In pollen access absent plots, we prevented flower access and olfactory cues by securing 16  $\times$  14 cm Glad Fold-Top plastic bags (Glad Products, Oakland, California, USA) around all cordgrass flowers with cable ties. In pollen access present plots, we did not inhibit ladybeetle access to cordgrass flowers. However, we controlled for the presence of cable ties in pollen access absent plots by applying cable ties to all stems in all plots. Additionally, our field manipulations recreated realistic habitat heterogeneity by interspersing plots from each treatment with each other (S. A. Rinehart and J. Walker, unpublished data).

We maintained our experiment for two weeks and monitored adult ladybeetle density in all plots on 12 September 2015. We determined adult ladybeetle density using two-minute timed searches. During these searches, we examined all stems in each plot. Adult ladybeetle densities were log-transformed to achieve assumptions of normality. We compared adult ladybeetle density between treatments using an analysis of covariance with scale insects (present/absent) and pollen access (present/absent) as fixed factors and cordgrass stem density as a covariate. We concluded our analysis with a Tukey's honestly significant difference post hoc test. We conducted all statistical analyses in JMP v. 13 (www.jmp.com).

#### *Effects of ladybeetle habitat use on adult performance*

*Assay design.*—For all performance assays, we reared ladybeetles on resources using a 2  $\times$  2 fully factorial design that manipulated scale

insects (present/absent) and pollen access (present/absent). We collected ladybeetles and flowering, scale-infested cordgrass stems (clipped at the air–soil interface) from SDL two hours prior to the study. We manipulated collected cordgrass stems to represent one of the four habitat treatments. In the scale insect absent treatment, we removed all scale insects from cordgrass stems using a soft toothbrush (Long and Porturas 2014, Rinehart et al. 2017). In the scale insect present treatment, we did not alter the density of scale insects on cordgrass stems. In the pollen access absent treatment, we placed all cordgrass flowers in 4  $\times$  4 cm (length  $\times$  width; with 2 mm openings) bags and secured them with cable ties. In the pollen access present treatment, we did not restrict ladybeetle access to cordgrass flowers. We controlled for the presence of cable ties in the pollen access absent treatment by applying them to all stems included in the study. We then placed the clipped ends of modified cordgrass stems into 13  $\times$  13 cm (height  $\times$  diameter) cylindrical plastic containers filled with 700 mL of tap water and enclosed whole cordgrass stems in 54  $\times$  13 cm (length  $\times$  width) bags made with white nylon insect mesh (6 mm mesh opening). Finally, we introduced a single adult ladybeetle into each replicate, using only mated females in the fecundity assay and both sexes in the longevity assay. To prevent resource depletion in replicates, we replaced modified cordgrass stems weekly. All replicates were maintained at a mean temperature of 21.1°C with a 12:12-h light–dark cycle ( $85.6 \pm 5$   $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  [PAR]; Philips Natural Light 40W).

*Fecundity.*—To understand how female ladybeetle fecundity is influenced by resource-dependent habitat use, we conducted four separate, two-week-long trials ( $n = 5$ /treatment per trial) between 10 July 2015 and 03 September 2015. We ran multiple trials due to the difficulty of obtaining enough mated females during a single collection period. We monitored replicates daily for the presence of eggs. When eggs were found, we counted the number of individual eggs in each clutch. We then collected clutches and placed them in separate 50-mL beakers with 6-mm nylon mesh covering the top. We monitored clutches daily until eggs hatched. We recorded the total number of larvae produced. We analyzed the number of eggs laid and larvae

produced per adult female ladybeetle using separate Kruskal–Wallis one-factor analysis of variance, with habitat treatment (i.e., scale insects absent, pollen access absent; scale insects absent, pollen access present; scale insects present, pollen access absent; and scale insects present, pollen access present) as a factor and used a Steel–Dwass post hoc test where necessary.

*Adult longevity.*—To understand how adult ladybeetle longevity is affected by resource-dependent habitat use, we monitored adult ladybeetle survival daily between 24 August 2014 and 02 November 2014, when the last ladybeetle died. We analyzed adult ladybeetle longevity using the Cox proportional hazards model with an effect likelihood ratio test for two categorical covariates, scale insects (present/absent) and pollen access (present/absent).

#### *Effects of adult ladybeetle habitat use on larval longevity*

To assess how habitat use affects larval ladybeetle survival, we collected first-instar larvae (<12 h old) from eggs produced by female ladybeetles in our reproductive fitness trials. To minimize impacts of maternal habitat on larval longevity, we allocated larvae from mothers in different habitat treatments evenly across our four larval habitat treatments: (1) scale insects absent, pollen access absent ( $n = 25$ ); (2) scale insects present, pollen access absent ( $n = 24$ ); (3) scale insects absent, pollen access present ( $n = 25$ ); and (4) scale insects present, pollen access present ( $n = 21$ ). We provided all replicates with one whole cordgrass leaf with scale insects (present/absent). Additionally, we manipulated pollen access (present/absent) by providing ladybeetle larvae access to a cordgrass flower or no flower. We replaced habitat resources every three days to prevent cordgrass tissues from desiccating. We maintained all replicates at a constant temperature of 20°C with a 12:12-h light–dark cycle ( $85.6 \pm 5 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  [PAR]; Philips Natural Light 40W). We monitored larval ladybeetle survival daily between 15 July 2015 and 02 September 2015. We analyzed larval ladybeetle longevity using the Cox proportional hazards model with an effect likelihood ratio test for two categorical covariates, scale insects (present/absent) and pollen access (present/absent).

#### *Effects of environmental cues on ladybeetle habitat use*

To test whether ladybeetle preference for olfactory cues matched their habitat use, we conducted a series of paired-choice assays in a Y-tube olfactometer between June and August 2014. In the olfactometer, we provided adult ladybeetles with the choice of airborne cues from cordgrass leaves vs. blank air ( $n = 32$ ), cordgrass leaves vs. *Sarcocornia pacifica* (hereafter, pickleweed) leaves ( $n = 24$ ), and cordgrass leaves with vs. without scale insects ( $n = 25$ ). We compared adult ladybeetle preference of cordgrass and pickleweed olfactory cues, because pickleweed is the second most abundant plant species in ladybeetle habitat (J. D. Long, S. A. Rinehart, and J. Walker, unpublished data). It is important to note that only cordgrass leaves were used in olfactory trials and that cordgrass flowers were not tested. In all plant treatments, we used three leaves as the volatile chemical source. Plant leaves were harvested from whole cordgrass stems and pickleweed plants transplanted from Sweetwater Marsh (South San Diego Bay; 32°38'15.8" N, 117°06'37.5" W) on 28 May 2014. Harvested plants were stored at the Coastal and Marine Institute Laboratory in outdoor flow-through seawater tables until they were used. Plants were only used once as a volatile source then discarded. Adult ladybeetles were collected within 12 h of trials from SDL and were provided scale insects and cordgrass pollen ad libitum until use. Prior to each trial, we randomly assigned treatments to one of two cylinders attached to the arms of the Y-tube olfactometer and calibrated the air flow rates in both arms to 200 ml/min (Zhang et al. 2009). We cleaned the Y-tube olfactometer with 95% ethanol between every trial (Zhang et al. 2009).

In each trial, we placed a single adult ladybeetle at the end of the base tube and observed ladybeetle behavior for 30 min (Bahlai et al. 2008). We recorded an outcome only after the ladybeetle crossed the decision line, which was defined as 5 cm up either arm of the Y-tube, and remained there for at least 30 s (an approach consistent with previous Y-tube olfactometer studies involving ladybeetles, e.g., Bahlai et al. 2008). If a ladybeetle failed to make a decision after 30 min, we marked the trial as no response and excluded it from our analyses. We analyzed

ladybeetle choices using binomial exact tests for each assay.

## RESULTS

### *Effects of resource availability on ladybeetle habitat use*

Habitat manipulations influenced adult ladybeetle density (Fig. 1;  $F_{3,25} = 3.29$ ,  $P = 0.013$ ). Adult ladybeetles were 2.7 times more abundant in plots with scale insects ( $F_{1,25} = 17.23$ ,  $P < 0.001$ ; Appendix S1: Table S1). We found no effect of pollen access on adult ladybeetle density ( $F_{1,25} = 0.42$ ,  $P = 0.533$ ). There was no interaction between scale insects and pollen access ( $F_{1,25} = 1.21$ ,  $P = 0.282$ ). However, there was a trend for plots containing both scale insects and access to cordgrass pollen to have the greatest density of adult ladybeetles. Finally, cordgrass stem density had no effect on the density of adult ladybeetles in habitat patches ( $F_{1,25} = 0.64$ ,  $P = 0.43$ ).

### *Effects of ladybeetle habitat use on adult performance*

*Fecundity.*—Habitat resources critically affected ladybeetle egg production in the laboratory (Fig. 2A;  $\chi^2 = 15.769$ ,  $df = 3$ ,  $P = 0.001$ ). Female ladybeetles with access to scale insects laid 10 times more eggs than females lacking access to scale insects ( $8.81 \pm 1.5$  and  $0.88 \pm 1.5$ , respectively; mean  $\pm$  SE). However, for treatments with

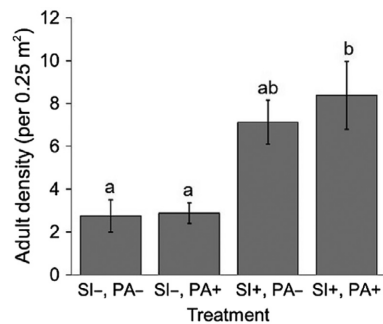


Fig. 1. Mean ( $\pm$ standard error) adult ladybeetle density in manipulated habitat plots. Habitat treatments ( $n = 8$ ) are as follows: scale insect present (SI+), scale insect absent (SI-), pollen access present (PA+), and pollen access absent (PA-). Treatments with shared letters are not significantly different at an  $\alpha = 0.05$  (Tukey's honestly significant difference test).

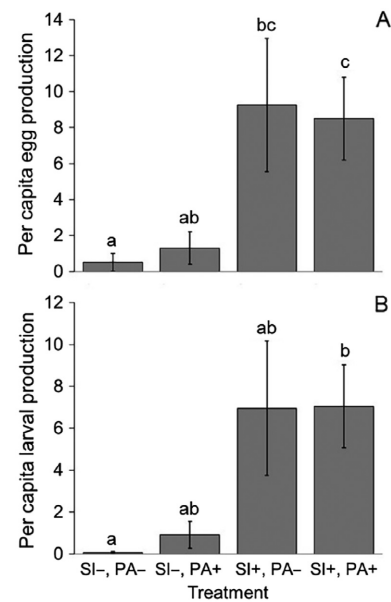


Fig. 2. Mean ( $\pm$ standard error) per capita (A) egg production and (B) larval production in each habitat resource treatment ( $n = 20$ ). Scale insect present (SI+), scale insect absent (SI-), pollen access present (PA+), and pollen access absent (PA-). Treatments with shared letters are not significantly different at an  $\alpha = 0.05$  (Steel–Dwass test).

scale insects, egg production did not depend upon pollen access at  $\alpha = 0.05$  (Steel–Dwass test for scale insect present, pollen access absent and scale insect absent, and pollen access present treatments;  $P = 0.064$ ).

Similarly, habitat resources determined larval ladybeetle production (Fig. 2B;  $\chi^2 = 13.732$ ,  $df = 3$ ,  $P = 0.003$ ). Female ladybeetles with access to scale insects produced  $\sim 15\times$  more larvae than ladybeetles lacking access to scale insects ( $7.0 \pm 1.9$  and  $0.48 \pm 0.32$ , respectively; mean  $\pm$  SE). However, for treatments with scale insects, larval production did not depend upon pollen access at  $\alpha = 0.05$  (Steel–Dwass test for scale insect present, pollen access absent and scale insect absent, and pollen access present treatments;  $P = 0.07$ ).

*Adult longevity.*—Habitat resources determined adult ladybeetle longevity ( $\chi^2 = 10.0$ ,  $df = 3$ ,  $P = 0.02$ ). Specifically, adult ladybeetles lived longer when they had access to either scale insects or pollen (Fig. 3; scale insects,  $\chi^2 = 5.41$ ,  $df = 1$ ,  $P = 0.02$ ; pollen,  $\chi^2 = 5.11$ ,  $df = 1$ ,  $P = 0.024$ ).

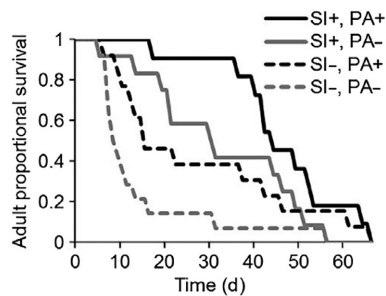


Fig. 3. The proportional survival of adult ladybeetles in each habitat resource treatment ( $n = 15$ ). Treatments are as follows: scale insect present (SI+), scale insect absent (SI-), pollen access present (PA+), and pollen access absent (PA-).

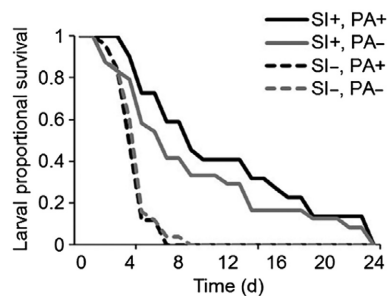


Fig. 4. The proportional survival of larval ladybeetles in each habitat resource treatment. Treatments are as follows: scale insect present (SI+), scale insect absent (SI-), pollen access present (PA+), and pollen access absent (PA-). Sample size is 25 for scale insect absent treatments, 24 for the scale insect present, pollen access absent treatment, and 21 for the scale insect present, pollen access present treatment.

However, we found no significant interaction between scale insects and pollen access ( $\chi^2 = 0.64$ ,  $df = 1$ ,  $P = 0.424$ ), despite individuals in scale insect present, pollen access present habitats

tending to have the greatest longevity ( $45.9 \pm 5$  d, mean  $\pm$  SE). Ladybeetles provided either scale insects or pollen (but not both) had similar mean longevity, with individuals surviving  $32.2 \pm 4.8$  and  $27.2 \pm 4.6$  d, respectively. Finally, ladybeetles without access to scale insects or pollen had the shortest longevity, surviving only  $13.8 \pm 4.4$  d.

#### Effects of adult ladybeetle habitat use on larval longevity

Habitat resources strongly impacted the longevity of larval ladybeetles (Fig. 4,  $\chi^2 = 23.99$ ,  $df = 3$ ,  $P < 0.001$ ). Specifically, larval ladybeetles with access to scale insects survived  $2\times$  longer than larvae without access to scale insects ( $\chi^2 = 23.88$ ,  $df = 1$ ,  $P < 0.001$ ). Pollen access had no effect on larval longevity ( $\chi^2 = 0.04$ ,  $df = 1$ ,  $P = 0.846$ ). Additionally, we found no interaction between scale insects and pollen on larval longevity ( $\chi^2 = 0.613$ ,  $df = 1$ ,  $P = 0.434$ ).

#### Effects of environmental cues on ladybeetle habitat use

Adult ladybeetles were more attracted to chemical cues associated with scale-free cordgrass leaves relative to cue-free controls (Table 1,  $P < 0.001$ ) or chemical cues from pickleweed ( $P < 0.001$ ). Additionally, adult ladybeetles were 14 times more likely to be attracted to chemical cues from cordgrass leaves with scale insects than cordgrass leaves without scale insects ( $P < 0.001$ ).

## DISCUSSION

Habitat use and performance were strongly linked for an ecologically important salt marsh consumer—ladybeetles preferentially used habitats that enhanced their reproductive output and

Table 1. Preferences of adult ladybeetles for odors from common marsh plant and insect resources.

Comparison	N	% Response	% Choice		P
			Arm 1	Arm 2	
Cordgrass leaves vs. blank	34	64.7	77.3	22.7	<0.001
Cordgrass leaves vs. pickleweed leaves	24	79.1	79.0	21.0	<0.001
Cordgrass leaves with scale insects vs. cordgrass leaves without scale insects	25	60.0	93.3	7.7	<0.001

Notes: Outcomes were analyzed using binomial exact tests. % Response values were calculated using the proportion of trials resulting in ladybeetle choice divided by the total trials run (including trials where no choice was made). % Choice values were calculated by dividing the number of trials resulting in a specific habitat choice by the number of trials where ladybeetles made any choice (i.e., trials where beetles made no choice were removed).

longevity. Ladybeetle habitat use increased in the presence of scale insects and, to a lesser extent, cordgrass pollen (Fig. 1). In the laboratory, scale insect prey increased adult ladybeetle survival and reproductive output, but cordgrass pollen only enhanced adult ladybeetle survival (Figs. 2, 3). Similarly, scale insects were essential for the survival of larval ladybeetles (Fig. 4).

Such strong links between habitat use and performance may exist for these ladybeetle consumers for two reasons. First, there should be strong selective pressures on female ladybeetles to oviposit in habitats containing scale insects because of their influence on egg production (48% of females with access to scale insects laid eggs compared to only 1% of females lacking scale insect access) and larval longevity (larvae in habitats with scale insects survived 2.2 times longer than those in habitats lacking scale insects). Selective pressures on oviposition in this system may be exacerbated by the fact that larval ladybeetles are relatively immobile compared to adults (S. A. Rinehart, *personal observation*). This relative lack of mobility may prevent larvae from correcting errors in maternal oviposition choice. Therefore, female ladybeetle habitat use should have direct consequences on their overall reproductive success.

Second, positive correlations between habitat use and performance may be more common for top consumers, as their distributions should not be influenced by predation risk. Indeed, it is well-documented that habitat use can be altered in the presence of predation (Werner et al. 1983, Brown 1988, Lima and Dill 1990, Heithaus and Dill 2002). For example, bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, preferentially use safe deep habitats over risky shallow habitats when tiger sharks (*Galeocerdo cuvier*) are present (Heithaus and Dill 2002). In our system, ladybeetles are likely top consumers, as previous work has suggested that ladybeetles are unacceptable prey for most common predators (Frazer and Rothschild 1960, Daloz et al. 1994). Therefore, ladybeetles should have limited predation risk, allowing their habitat use to be determined by other factors such as resource availability.

In laboratory olfactory trials, adult ladybeetles were able to distinguish between chemical cues from cordgrass leaves with and without scale

insects. In fact, adult ladybeetles were 14 times more likely to move toward cordgrass leaves with scales insects than without them. This suggests that ladybeetles may use chemical cues from scale insect-infested cordgrass to inform their habitat selection over small spatial scales.

While scale insects were the primary driver of ladybeetle habitat use and performance, the availability of cordgrass pollen prevented adult ladybeetle starvation when no other resources were present (i.e., SI-PA+ treatments). Pollen access also tended to increase adult ladybeetle survival when fed in conjunction with scale insects (Fig. 3). These findings suggest that pollen availability may facilitate local ladybeetle population growth by enhancing adult survival. If this is the case, there is value in timing marsh restoration projects with cordgrass flowering (e.g., July–September), as larger ladybeetle populations may increase the magnitude of ladybeetle predator effects (i.e., consumptive and nonconsumptive effects) on scale insects, thus minimizing scale insect effects on newly transplanted cordgrass stems (Rinehart et al. 2017).

The relationship between habitat use and individual performance should have clear implications for animal local population dynamics. For instance, positive relationships between habitat use and performance should maximize individual fitness and may enhance local population density (McLoughlin 2007, Gripenberg et al. 2010). Therefore, knowing the relationship between habitat use and performance should help identify particularly valuable habitats (or valuable habitat features) for a given species. This is especially important for guiding habitat management for ecologically important species (like ladybeetles). Here, we show scale insect prey enhanced ladybeetle performance and increased habitat use by ladybeetles. Overall, understanding relationships between ladybeetle habitat use and performance should aid salt marsh managers in identifying critical habitat for these ecologically important consumers.

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