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Title: Mixed effects of an introduced ecosystem engineer on the foraging behavior and habitat selection of predators

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Running Head: Divergent effects of introduced engineer

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Abstract

Invasive ecosystem engineers both positively and negatively affect their recipient ecosystems by generating novel habitats. Many studies have focused on alterations to ecosystem properties and **This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1002/ecy.2495](https://doi.org/10.1002/ecy.2495)**

28 to native species diversity and abundance caused by invasive engineers. However, relatively few
29 studies have documented the extent to which behaviors of native species are affected. The red
30 seaweed *Gracilaria vermiculophylla* (Rhodophyta) invaded estuaries of the southeastern United
31 States within the last few decades and now provides abundant aboveground vegetative cover on
32 intertidal mudflats that were historically devoid of seaweeds. We hypothesized that *G.*
33 *vermiculophylla* would affect the foraging behavior of native shorebirds positively for birds that
34 target seaweed-associated invertebrates or negatively for birds that target prey on or within the
35 sediment now covered with seaweed. Visual surveys of mudflats >1 ha in size revealed that more
36 shorebirds occurred on mudflats with *G. vermiculophylla* relative to mudflats without *G.*
37 *vermiculophylla*. This increased density was consistent across 7 of 8 species, with the one
38 exception being the semipalmated plover *Charadrius semipalmatus*. A regression-based analysis
39 indicated that while algal presence predicted shorebird density, densities of some bird species
40 depended on sediment composition and infaunal invertebrate densities. At smaller spatial scales
41 (200 m² and <1 m²), experimental removals and additions of *G. vermiculophylla* and focal
42 observations showed strong variation in behavioral response to *G. vermiculophylla* among bird
43 species. Birds preferentially foraged in bare mud (e.g., *C. semipalmatus*), in *G. vermiculophylla*
44 (e.g., *Arenaria interpres*), or displayed no preference for either habitat (e.g., *Tringa*
45 *semipalmata*). Thus, while the presence of the invasive ecosystem engineer on a mudflat
46 appeared to attract greater numbers of these predators, shorebird species differed in their
47 behavioral responses at the smaller spatial scales that affect their foraging. Our research
48 illuminates the need to account for species identity, individual behavior, and scale when
49 predicting impacts of invasive species on native communities.

50

51 **Keywords:** ecosystem engineers; estuaries; foraging behavior; foundation species; habitat-
52 modifying species; niche; non-native species; novel ecosystems; shorebirds; soft sediment

53

54 **Introduction**

55 Invasive species are one of the leading threats to global and local biodiversity (Vitousek
56 et al. 1996); yet, their effects are often nuanced, affecting native species both negatively and
57 positively by altering resource availability and quality, trophic interactions, and disturbance
58 regimes (e.g., Straube et al. 2009; Byers et al. 2010; Simberloff 2011; Simberloff et al. 2013;

59 Pintor and Byers 2015). Invasive species can have particularly far-reaching effects if they are
60 ecosystem engineers – organisms that directly or indirectly regulate the availability of resources
61 through physical state changes within an ecosystem (Jones et al. 1994, 1997; Crooks 2002).
62 Their control of food and habitat resources makes invasive ecosystem engineers fundamental
63 determinants of the diversity and abundances of native species (e.g., Di Tomaso 1998; Grosholz
64 et al. 2009; Villamagna and Murphy 2010; DeVore and Maerz 2014).

65 Ecosystem engineers can disproportionately affect community structure, as these
66 organisms influence both bottom-up and top-down controls. The effects of an invasive
67 ecosystem engineer may be even more conspicuous because the invasive engineer may exert
68 mixed effects through a variety of mechanisms that can ultimately transform whole ecosystems
69 as they settle into new equilibria (Byers et al. 2010). Despite the potential for negative
70 consequences of invasive ecosystem engineers during system transformation, they can positively
71 affect native community members through generation of habitat (e.g., Gribben et al. 2013;
72 DeVore and Maerz 2014; Wright et al. 2014). Furthermore, the relative contribution of negative
73 and positive effects is dependent on the context in which the ecosystem engineer is introduced
74 (Guy-Haim et al. 2018). For example, in southeastern Appalachian forests, the invasion of
75 herbaceous understory communities by Japanese stilt grass (*Microstegium vinineum*) has mixed
76 effects on some native community members. The increased habitat complexity reduces arthropod
77 density (Simoa et al. 2010) on the forest floor, but increases habitat availability for predatory
78 spiders (DeVore and Maerz 2014). Both effects reduce populations of amphibians (DeVore and
79 Maerz 2014). Thus, studies of community-level interactions are important when identifying the
80 potential mixed effects of invasive ecosystem engineers.

81 Positive effects of invasive ecosystem engineers can result when the habitats that they
82 provision are different in kind from the structure that is naturally available (Crooks 2002). For
83 instance, novel ecosystem engineers may provide new habitat structure that shifts prey
84 distributions to areas with greater structural complexity (Tanner 2011). In fact, a review of
85 facilitation of native species by invasive species identified habitat modification, specifically the
86 creation of novel habitat, as the most frequently cited mechanism for these facilitative
87 interactions (Rodriguez 2006). Furthermore, the introduction of structure by an invasive species
88 could be more pronounced if structure is a limiting factor in the community. Such alterations in
89 habitat quality and subsequent bolstering of native species may have cascading effects on an

90 ecosystem's trophic structure. For instance, zebra mussels, *Dreissena polymorpha*, which
91 provide novel structure and refuge in the benthic zones of freshwater lakes, house exponentially
92 greater numbers of invertebrates than *D. polymorpha*-free substrate (Bially and MacIsaac 2000;
93 Rodriguez 2006; Sousa et al. 2009). The greater abundance of food items in the invaded areas
94 has led to increased growth rates of benthic consumers (Thayer et al. 1997; Rodriguez 2006).
95 Not only can habitat modification lead to changes in overall prey abundance, it can also cause
96 predators to change their preferences for foraging habitat. For example, the invasive tubeworm,
97 *Ficopomatus enigmaticus*, creates reef structures that attract greater densities of invertebrates and
98 increases shorebird foraging in the novel habitat (Schwindt et al. 2001; Bruschetti et al. 2009).
99 Such positive interactions are not necessarily the norm, and these interactions and subsequent
100 impacts are likely to be highly dependent on scale, history of invasion, and local community
101 dynamics (Jones et al. 1997).

102 Another consideration when assessing how an ecosystem engineer may influence a
103 recipient environment is how resident species distinctively respond to novel structure. For
104 example, native species with different ecological niches may perceive the environmental
105 modifications by invasive ecosystem engineers differently, suggesting the possibility of mixed
106 effects across a community (e.g., Crooks 1998). Distinguished alterations of species behaviors
107 can in turn lead to shifts in species interaction strengths for fundamental processes, like
108 predation. Because predator identity and diversity are known to determine trophic structure by
109 altering behavior and abundances of lower trophic levels (Bruno and O'Connor 2005; O'Connor
110 et al. 2008), predator species reacting differently to an invasive ecosystem engineer could create
111 effects that cascade through the food web. Thus, when assessing the effect of an invasive
112 ecosystem engineer on native communities, it is important to recognize that species and
113 individuals may respond distinctively. Additionally, determining the effects of invasive species
114 on multiple predator species could reveal whether niche differentiation or behavioral differences
115 produce divergent responses among a suite of predators that utilize the same prey resources.
116 Here, we examine the responses of multiple native species within the same trophic level to a
117 ubiquitous introduced ecosystem engineer. Such comparisons may elucidate the degree of
118 variation in overall response by the native community and may help to predict responses of
119 individual species based on their foraging ecology and ecological roles within the community.

120 *Research System and Questions*

121 A recent ecosystem engineer invasion in the southeastern United States provides an
122 opportunity to investigate the roles these species play in recipient communities, specifically their
123 roles in the foraging patterns of multiple predator species within the same trophic level.
124 *Gracilaria vermiculophylla*, a red seaweed from the coast of Japan, has invaded many coastal
125 habitats in Europe and North America (Thomsen et al. 2009; Kim et al. 2010; Krueger-Hadfield
126 et al. 2017). Since the early 2000s, the invasive seaweed has considerably altered estuaries of
127 Georgia by creating novel habitat on the previously bare mudflats (Byers et al. 2012). This
128 system was largely devoid of macroalgae due to high turbidity and lack of hard substrate for
129 algal attachment. The alga is anchored on mudflats due to an association with native tube-
130 building polychaete worms, *Diopatra cuprea*, that attach the alga to their tubes (Thomsen and
131 McGlathery 2005; Berke 2012; Byers et al. 2012; Kollars et al. 2016). Increased habitat structure
132 and more amenable abiotic conditions (reduced surface temperatures and desiccation stress
133 during low tide) created by *G. vermiculophylla* have increased abundance of epifaunal
134 invertebrates and shifted many of their distributions from bare mudflats to those colonized by the
135 invasive seaweed (Byers et al. 2012; Wright et al. 2014; Bishop and Byers 2015).

136 In these estuaries, migratory shorebirds are important predators and are pivotal in
137 regulating macroinvertebrate abundances (Schneider and Harrington 1981; Steinmetz et al.
138 2003). Mudflat ecosystems provide shorebirds with high quality, often preferred, foraging habitat
139 (Burger et al. 1977; Lorenço et al. 2015). Furthermore, the estuaries of the southeastern U.S.
140 serve as important stopover and over-wintering sites for many shorebird species that migrate
141 between the Arctic and the tropics using the Atlantic Flyway. The most common shorebird
142 species found in the southeast during the peak migratory season (April-May) are dunlin (*Calidris*
143 *alpine*), semipalmated plover (*Charadrius semipalmatus*), western sandpiper (*Calidris mauri*),
144 least sandpiper (*Calidris minutilla*), semipalmated sandpiper (*Calidris pusilla*), ruddy turnstone
145 (*Arenaria interpres*), willet (*Tringa semipalmata*), black-bellied plover (*Pluvialis squatarola*),
146 and short-billed dowitcher (*Limnodromus griseus*) (Tomkins 1965; Stinson 1980; Harrington
147 2008; Rose and Nol 2010; L. Haram, *personal observation*). Shorebirds form dense
148 aggregations of mixed species that forage on intertidal mudflats during low tide. Niche
149 differentiation in these aggregations is achieved in part because each species has distinct
150 foraging strategies (visual, tactile, or mixed) and feeding morphologies (body and bill size and
151 shape) to catch epifaunal, epibenthic, and/or infaunal invertebrates in estuarine systems

152 (Mouristen 1994; Nettleship 2000; Jehl et al. 2001; Elner et al. 2005; Nebel et al. 2005; Thomas
153 et al. 2006; Nebel and Cooper 2008; Hicklin and Gratto-Trevor 2010; Rose and Nol 2010;
154 Lowther et al. 2011; Nol and Blanken 2014; Poole et al. 2016).

155 Shorebird species and community composition are non-randomly distributed within
156 estuarine habitats. The abundance, biomass, and availability of prey are crucial predictors of
157 shorebird communities on intertidal mudflats (Dugan et al. 2003; Spruzen et al. 2008; VanDusen
158 et al. 2012), with shorebirds known to forage in areas with greater prey availability (Fraser et al.
159 2010). Across microhabitats and entire mudflats, prey availability is constrained directly by
160 abiotic factors, such as sediment composition and tidal cycle (Burger et al. 1977; VanDusen et al.
161 2012). Presence of vegetation on mudflats also influences shorebird distributions due to its
162 effects on macroinvertebrate abundance and shorebird foraging efficiency. Increased benthic
163 structure provided by submerged macrophytes, such as seaweeds, seagrasses, and reef-forming
164 fauna, can increase macroinvertebrate abundances (Spruzen et al. 2008; Bruschetti et al. 2009),
165 possibly leading to greater densities of birds utilizing invaded mudflats. Macrophytic wrack
166 subsidies to low productivity beaches can also increase availability of prey items for shorebirds,
167 with positive relationships observed between standing crop of wrack and shorebird abundances
168 (Dugan et al. 2003). However, dense macrophyte coverage on a mudflat may inhibit shorebird
169 foraging, likely through interference with tactile and visual detection of prey, smothering of
170 resources, and alteration of prey species composition (Spruzen et al. 2008). Given these
171 scenarios, the effect of an invasive habitat modifier on shorebird foraging could be mixed.
172 Furthermore, the impact of an ecosystem engineer may differ among predator species, causing
173 divergent, species-specific responses in foraging behavior and habitat selection.

174 Shorebirds present an optimal target for investigating the effects of invasive ecosystem
175 engineers like *G. vermiculophylla* on predator foraging because shorebirds adjust to local
176 conditions, feed opportunistically, and shift their prey preferences with season and local prey
177 availability (Dierschke et al. 1999; Nettleship 2000; Jehl et al. 2001; Nebel and Cooper 2008;
178 Hicklin and Gratto-Trevor 2010; Mathot et al. 2010; Rose and Nol 2010; Lowther et al. 2011;
179 Poole et al. 2016). Through two observational studies and two complementary manipulative
180 experiments at various spatial scales, we assessed how the novel physical structure of an invasive
181 ecosystem engineer alters shorebird foraging in essential stopover habitat. We hypothesized that
182 the presence of *G. vermiculophylla* would have significant effects on the density of shorebirds,

183 with shorebirds preferring mudflats inhabited by the invasive engineer due to greater prey
184 availability. However, we also hypothesized that alterations in foraging behavior would be
185 species-specific depending on each species' niche type. Despite the potential for mixed effects,
186 we expected net positive relationships between the invasive ecosystem engineer and shorebird
187 density and foraging effort, given the higher epifauna abundance associated with *G.*
188 *vermiculophylla*, shorebirds' opportunistic foraging during migration, and the limited physical
189 impediment we expected the alga would present. We intended our multi-species perspective to
190 elucidate the degree of uniformity (or lack thereof) in the behavioral responses of higher trophic
191 levels to invasive ecosystem engineers.

192 **Methods**

193 *Large Scale Habitat Selection Survey*

194 To determine what habitat type (*Gracilaria*-colonized or bare mudflats) was more
195 attractive to shorebirds, we conducted shorebird density surveys across twelve mudflats in
196 Wassaw Sound, Savannah, Georgia (31°56'18.8"N, 80°56'53.7"W): six mudflats with *G.*
197 *vermiculophylla* and six mudflats without *G. vermiculophylla* (Appendix S1: Table S1). We
198 selected sites based on size (>1 ha), continuity of substrate, and observer access. During tides
199 below 0 m mean lower low water (MLLW) in daylight hours, we surveyed 500 m transects
200 parallel to the water line for shorebird abundance and species composition at each site. Along the
201 transect, we surveyed the entire width of the intertidal mudflat from the low tide line to its
202 highest elevation, which was visually determined based on water level predictions, time of day,
203 and biological zonation of *Spartina* cord grass or oyster reef. The location of the 500 m transect
204 was selected using low tide images on Google Earth, and clear landscape features were used as
205 end points for the transect. Surveys were done by boat (and in one instance by foot due to
206 logistical issues) ~50 m away. Care was taken to not flush the flocks, and no apparent
207 disturbance of shorebird activity was detected across survey sites. A captain maintained a slow,
208 consistent speed while a trained observer counted birds using 16x50 Nikon 7247 Action
209 binoculars. A single observer identified and counted shorebirds across sites to eliminate observer
210 differences and minimize potential error. Small sandpiper species (*Calidris spp.*) (approximately
211 <17 cm in length) were counted collectively as "Peeps" because the distance from the mudflats,
212 speed of surveys, and winter plumage was not conducive to further identification. To standardize
213 conditions between sites, we conducted surveys on days when weather was fair, with no

214 precipitation and wind speed < 20 knots. We surveyed each mudflat twice from April 2, 2015 to
215 May 17, 2015 (excluding two sites, House Creek and Little Tybee, that we surveyed once) for a
216 total of 22 surveys; surveys were averaged for each site to reduce the effect of sampling date.
217 Spring movement begins in March for these species, with their peak migrations through the
218 southeastern U.S. occurring in April to early May (see descriptions in Warnock and Gill 1996;
219 Nettleship 2000; Jehl et al. 2001; Nebel and Cooper 2008; Hicklin and Gratto-Trevor 2010;
220 Lowther et al. 2011; Nol and Blanken 2014; Poole et al. 2016). We attempted to standardize bird
221 counts by recording them at their highest levels (i.e., during peak migration). We standardized
222 the shorebird counts as densities by estimating the total area (hectares) of each mudflat spanned
223 by the 500 m transect using the polygon tool on low-tide images from Google Earth.

224 Because shorebirds are known to select foraging sites based on an array of conditions, we
225 gathered additional data on environmental and biotic variables at each surveyed mudflat that may
226 covary with *G. vermiculophylla* presence. Once we completed a shorebird survey, we established
227 a 50 m transect in the middle of the 500 m transect at approximately 0 MLLW, along which we
228 sampled *G. vermiculophylla* biomass density, epifaunal/epibenthic invertebrate density, infaunal
229 invertebrate density, and sediment composition every 5 m for a total of 10 sampling points per
230 site. To quantify *G. vermiculophylla* biomass and its associated epifaunal (i.e., found on
231 seaweed) and epibenthic (i.e., found on the sediment) invertebrates, we collected all *G.*
232 *vermiculophylla* in a 0.25 m² quadrat and immediately placed it in Ziploc bags for transport back
233 to the laboratory. We also recorded large epibenthic invertebrates (~1 cm and greater) in this
234 same quadrat found on the sediment surface. Directly adjacent to each quadrat, we collected
235 sediment cores (10 cm diameter, 10 cm deep) for abundance of infaunal and small epibenthic
236 invertebrates (referred to collectively as infauna hereafter) and cores for sediment composition (3
237 cm diameter, 8 cm deep).

238 In the lab, we rinsed the *G. vermiculophylla* gathered from the quadrat samples, removed
239 epifaunal and epibenthic invertebrates and preserved them in 10% buffered formalin. We then
240 weighed the seaweed for wet biomass (g) and dried it at 60 °C for a minimum of two days to
241 attain dry biomass (g). For the infaunal abundance sediment cores, we sieved the cores using 250
242 µm mesh and filtered seawater. We immediately sorted visible infauna and preserved them in
243 10% buffered formalin. We preserved the remaining sample for sorting under a dissection scope.
244 We later transferred all preserved samples to 80% ethanol. Due to high invertebrate abundances

245 in the sediment cores, only the first four infauna sediment cores from each site were processed.
246 We classified invertebrates based on their lowest identifiable taxonomy. After identification, we
247 dried the organisms in our sediment core samples at 60°C for 3 days and weighed the organisms
248 pooled by taxonomic unit for dry biomass (g). The ten sediment cores for sediment composition
249 were combined by site and processed for percent composition of sand, silt, and clay by the Soil,
250 Plant, and Water Laboratory at the University of Georgia.

251 To determine the relationship between shorebird density (shorebirds/ha), *G.*
252 *vermiculophylla* presence, and other environmental variables, we performed a linear regression
253 using the 'stats' package in R 3.3.2 (R Core Team 2016). The predictor variables included algal
254 presence (*Gracilaria* presence or absence), average infauna density (invertebrates/0.0079 m²),
255 average epifaunal/epibenthic invertebrate density (invertebrates/0.25 m²) and the ratio of percent
256 sand to percent silt. Sites that averaged less than 5 g dry weight of *G. vermiculophylla* were
257 categorized as absent of *G. vermiculophylla*. All continuous variables were natural log-
258 transformed to achieve normality based on visual inspection of distributions using the 'qqnorm'
259 function in 'stats' package in R (R Core Team 2016). Independent variables were analyzed for
260 correlation using the stepVIF function in the 'pedometrics' package in R (Samuel-Rosa 2015).
261 Epifaunal/epibenthic invertebrate density was correlated with algal presence in all bird species
262 models, and thus was excluded from the final model. We determined the relationship between
263 algal presence and shorebird density of all species pooled as well as for individual species. In
264 addition, we constructed all possible models and ranked them for best fit using an AICc
265 comparison in the 'AICcmodavg' package in R (Mazerolle 2017). We completed this analysis
266 again, replacing average invertebrate densities with average invertebrate biomass densities. We
267 included density and biomass predictors in separate models to reduce correlation effects.
268 Although biomass measurements were completed for the infaunal core data, we did not measure
269 biomass directly for the epifaunal/epibenthic quadrat data. Thus, we calculated the average per
270 capita biomass of different invertebrate phyla/classes in the infaunal cores and multiplied the
271 estimated per capita biomass by the total number of individuals of the corresponding taxon in the
272 epifaunal/epibenthic quadrat data. Results for the analysis with infaunal and epibenthic/epifaunal
273 biomass as predictor variables are presented in Appendix S1: Table S3.

274 To determine the effect of *G. vermiculophylla* presence on epifaunal/epibenthic and
275 infaunal invertebrate densities, we constructed generalized linear mixed effects models with

276 negative binomial distributions and zero-inflation in the ‘glmmADMB’ package (Bolker et al.
277 2013) in R, with site as a random effect. We also determined the effect of *G. vermiculophylla* on
278 epifaunal/epibenthic and infaunal invertebrate biomass densities, using linear mixed models with
279 site, again, as a random effect. We evaluated the effect of algal presence on epifaunal/epibenthic
280 invertebrates from the quadrat samples (total n = 120) and infaunal invertebrates from the
281 sediment core samples (total n = 48) separately due to the different collection methods.

282 *Intermediate Scale Habitat Selection - Experimental Removal and Addition of Seaweed*

283 Though abundance surveys provide essential information about shorebird habitat
284 association at the large scale (>1 ha), we wanted to experimentally examine how *G.*
285 *vermiculophylla* presence affects shorebirds’ habitat selection and foraging. Therefore, we
286 conducted manipulative field experiments at an intermediate scale (200 m²) to determine if the
287 birds foraged more in areas of *G. vermiculophylla* versus adjacent bare treatments. We ran the
288 first experiment over a three-week period in April 2014, on three *G. vermiculophylla*-inhabited
289 mudflats used in the habitat preference survey. We were unable to visit the three sites over
290 successive days due to the need for two consecutive days of fair weather (<20 knot winds and no
291 precipitation) and negative low tides (-0.5 to -1.0 MLLW) for each site. At each site, we
292 haphazardly selected a location on the mudflat and established two 10 x 20 m² plots separated by
293 10 m. The proximity of the plots was meant to reduce variability in abiotic and biotic conditions
294 between the plots and allowed for birds to encounter both plots in a short time period. We
295 removed *G. vermiculophylla* from one plot and left *G. vermiculophylla* intact in the other. To
296 remove *G. vermiculophylla* from the entire plot, while minimizing disturbance to the mud
297 surface, we moved through the plot at low tide on flat flotation boards. We controlled for
298 sediment disturbance by moving through the paired plots similarly and allowed the sediment to
299 settle over a full tidal cycle before beginning our observations. Over the duration of a low tide
300 (~3 hours), 3-minute focal bird observations were conducted for shorebirds that visited each
301 treatment. We observed each bird for up to three minutes, or until it left the plot, recording
302 number of pecks and overall time spent in the plot. We alternated observations between the
303 removal versus control plots. Observations were made from the mudflat, at least 20 m away from
304 the plots behind a mobile blind, using 16x50 binoculars. We standardized foraging effort by each
305 observed bird by assessing foraging rates (pecks/minute). In these experiments, peck rate is the

306 definitive response, as it depicts true foraging effort, while time spent in a plot may be a mixture
307 of foraging and meandering.

308 From mid-April to mid-May 2015, we conducted a reciprocal experiment by adding *G.*
309 *vermiculophylla* to experimental plots on three mudflats in Wassaw Sound where it was absent.
310 The contrast in the effect of *G. vermiculophylla* between this addition experiment and the
311 previous removal experiment should inform at least two factors. First, the contrast should allow
312 us to examine whether *G. vermiculophylla*'s presence or absence at a mudflat scale (i.e., the
313 background context) influences bird foraging decisions on the smaller, experimental-plot scale.
314 Second, the contrast suggests whether *G. vermiculophylla* addition immediately affects shorebird
315 habitat preference or whether its influence accrues over time (e.g., through recruitment of
316 invertebrates). For this experiment, we left one of the paired plots as natural bare mudflat and to
317 the other we added a standard amount of *G. vermiculophylla* (~7 kg wet biomass). This amount
318 was the same amount of *G. vermiculophylla* that we removed from our highest density *G.*
319 *vermiculophylla* mudflat in the removal experiment. Using flat flotation boards, we added *G.*
320 *vermiculophylla* to the plot in a haphazard manner, attempting to create a natural spread of the
321 seaweed across the plot. *G. vermiculophylla* was secured in place through partial burial and
322 garden pins. Both plots were similarly disturbed and a similar number of garden pins were added
323 to each plot. We harvested seaweed for the *G. vermiculophylla* addition treatment from a single
324 site to ensure standard quality as well as epifauna within the *G. vermiculophylla*. We kept
325 epifauna intact to mimic conditions on a high-density *G. vermiculophylla* mudflat. We used the
326 same data collection methods and response variables as in the removal experiment.

327 We analyzed data for each experiment separately with a mixed-effects linear regression
328 model in R, using the 'lme4' package (Bates et al. 2015). For both experiments, the response
329 variable, pecks/minute, was natural log-transformed to attain normality and assessed as a
330 function of treatment (*G. vermiculophylla* vs. bare mud). We also analyzed the amount of time
331 (seconds) spent foraging as a function of treatment using a generalized linear regression analysis
332 with a negative binomial distribution. For analyses of both response variables, we treated site as
333 a random effect. Due to the lack of uniform presence of all shorebird species across sites, we first
334 examined foraging rates (pecks/minute) for all shorebirds pooled (removal: n = 68; addition: n =
335 92). We then performed species-specific analyses on the two most common species in our
336 experimental plots, dunlin (removal: n = 24; addition: n = 35) and semipalmated plovers

337 (removal: n = 15; addition: n = 23). Semipalmated plovers were only present at one site for each
338 experiment, so for their analysis, we removed the random site factor and analyzed the data using
339 regression analyses without mixed effects.

340 *Patch Scale Foraging Behavior Study*

341 To determine if shorebirds utilize *G. vermiculophylla* at the smallest scale (i.e., individual
342 clumps of seaweed attached to a *D. cuprea* worm tube, <1 m²), we conducted a study that
343 assessed individual shorebird preference for foraging directly in *G. vermiculophylla* clumps
344 versus the bare mud interspersed between seaweed patches. This helped ascertain whether birds
345 at the larger scales of our study are attracted to *G. vermiculophylla* specifically for foraging
346 quality (e.g., because high densities of invertebrates are present in *G. vermiculophylla* patches)
347 or are just associating generally with areas invaded by *G. vermiculophylla* due to a larger scale
348 influence the seaweed has on the environment or another correlated characteristic. Thus,
349 studying foraging behavior at this small scale (<1 m²) allowed us to determine if the shorebirds'
350 habitat choices at the large scale (>1 ha) are related to their actual foraging preferences.

351 In March 2015, on five mudflats colonized by *G. vermiculophylla* (and used in the Large
352 Scale Habitat Selection Survey), we observed up to five individual shorebirds from each of the
353 most common shorebird species [dunlin, semipalmated plover, least sandpiper, ruddy turnstone,
354 willet short-billed dowitcher, least sandpiper, and “peeps” (as before, remaining sandpiper
355 species were pooled together)]. We systematically visited one flat per sampling day, over the
356 course of 17 days. Sampling days were not successive due to the need for fair weather and
357 negative low tides. During low tide, we observed a single focal bird for up to three minutes (or
358 until it flew away) using 16x50 binoculars. During that time, we recorded the number of pecks in
359 natural *G. vermiculophylla* patches versus the surrounding bare mudflat. To compare the
360 frequency of pecks in *G. vermiculophylla* to the seaweed's frequency on the mudflat, we
361 quantified *G. vermiculophylla* percent cover by photographing ten 0.25 m² quadrats during the
362 Large Scale Habitat Selection Survey. From the photographs, we estimated the ratio of *G.*
363 *vermiculophylla* to bare mud at each mudflat with the image analysis software ImageJ. We
364 estimated the average percent cover of each patch-type at each site and then averaged across all
365 sites to obtain an overall average percent cover of *G. vermiculophylla* versus bare mud.
366 Photographs of one site (Priest Landing) were lost and not included in this average; however, its
367 average *G. vermiculophylla* biomass (known from the Large Scale Habitat Selection Survey) was

368 within the range of the other sites. We used the ratio of percent cover of *G. vermiculophylla* to
369 bare mud (0.27:0.73) to determine if the observed distribution of pecks significantly differed
370 from the availability of patches in nature.

371 We analyzed the data using a hierarchical Bayesian analysis, designed specifically for
372 ecological count data, in the R 3.3.2 package ‘bayespref’ (Fordyce et al. 2011). With this
373 package, we estimated the strength of foraging preference for *G. vermiculophylla* patches versus
374 bare patches for each bird and each species. The ‘bayespref’ package is preferred to other non-
375 parametric methods because it directly estimates individual- and population-level preference,
376 while allowing for non-normal distribution, dependent data, and uneven design (Fordyce et al.
377 2011). We ran models for 5,000 generations, with 10 generation burn-ins, setting prior
378 distributions based on the expected distribution of pecks given the average proportion of percent
379 cover of *G. vermiculophylla* patches to bare mud patches across sites. We visually assessed
380 diagnostic plots of MCMC chain distributions to choose the most evenly mixed model. Once we
381 generated preference strengths for each species, we compared the credible intervals (evaluated at
382 95%) to the proportion of *G. vermiculophylla* cover to bare mud. If the credible intervals of a
383 species did not overlap the expected patch-type cover, the preference was considered significant.

384 **Results**

385 *Large Scale Habitat Selection Survey*

386 We observed a significant, positive association of *G. vermiculophylla* presence and
387 shorebird density (birds/ha) across all sites when shorebirds were pooled (LM: $F_{1,10} = 5.65$, $p =$
388 0.04 , $R^2 = 0.30$) (Fig. 1a). This pattern was similar when assessed for individual species. Dunlin,
389 black-bellied plovers, willets, and short-billed dowitchers showed positive relationships with *G.*
390 *vermiculophylla* (LM: [dunlin – $F_{1,10} = 6.32$, $p = 0.03$, $R^2 = 0.33$]; [black-bellied plover – $F_{1,10} =$
391 11.93 , $p < 0.01$, $R^2 = 0.50$]; [willet – $F_{1,10} = 15.23$, $p < 0.01$, $R^2 = 0.56$]; and [short-billed
392 dowitcher – $F_{1,10} = 14.67$, $p < 0.01$, $R^2 = 0.55$]; Fig. 1b, 1e, 1g, and 1h, respectively). Both peeps
393 and ruddy turnstones demonstrated positive trends with *G. vermiculophylla* presence ([peeps –
394 $F_{1,10} = 4.68$, $p = 0.06$, $R^2 = 0.25$] and [ruddy turnstone – $F_{1,10} = 4.07$, $p = 0.07$, $R^2 = 0.22$]; Fig. 1c
395 and 1d). Semipalmated plover densities did not differ significantly (LM: $F_{1,10} = 0.14$, $p = 0.71$,
396 $R^2 < 0.10$; Fig. 1f).

397 Algal presence yielded the best fit model for all birds collectively and for some individual
398 species in the AICc comparisons, including ruddy turnstones, black-bellied plovers and willet

399 (see Appendix S1: Table S2 for AICc results). Semipalmated plover density was best fit by the
400 null (intercept-only) model. Additionally, the null model was within two Δi for “all birds”, peeps
401 and ruddy turnstones. However, for “all birds”, the algal presence model was over twice the
402 Akaike weight of the null model. For ruddy turnstones and peeps, the algal presence-only model
403 had 0.7 and 0.9 greater Akaike weights (respectively) than the null models. Other biotic and
404 abiotic variables also accounted for variance in the top models for dunlin, peep, willet, and short-
405 billed dowitcher densities. Dunlin densities were best fit by an additive model that included
406 positive effects of the ratio of percent sand to silt ($p < 0.01$) and infauna density ($p = 0.04$). Peep
407 densities were also best fit by an additive model of the ratio of percent sand to silt ($p < 0.01$) and
408 infauna density ($p = 0.05$), both of which were positively related to peep density. For short-billed
409 dowitchers, the best-fit model contained a significant negative interaction ($p < 0.01$) between
410 algal presence ($p < 0.01$) and the ratio of percent sand to percent silt ($p = 0.11$).

411 Differences in the distributions of epibenthic/epifaunal and infaunal invertebrates were
412 detected in response to *G. vermiculophylla* presence. When assessing epibenthic and epifaunal
413 invertebrate abundances, we found that mudflats with *G. vermiculophylla* had greater
414 epibenthos/epifauna densities (GLMM: $\chi^2_1 = 74.99$, $p < 0.01$, total $n = 120$; Appendix S1: Table
415 S4) and biomass densities (LMM: $\chi^2_1 = 12.99$, $p < 0.01$; Appendix S1: Table S5). *Gammarus*
416 *mucronatus* was the most abundant invertebrate within the quadrat samples (Appendix S1: Table
417 S4), while gastropods accounted for the greatest biomass (Appendix S1: Table S5). However,
418 when assessing infauna densities, we found no difference between *G. vermiculophylla* mudflats
419 and bare mudflats (GLMM: $\chi^2_1 = 0.42$, $p = 0.50$, total $n = 48$; Appendix S1: Table S6).
420 Similarly, we found no difference in infauna biomass between the two habitat types (LMM: χ^2_1
421 $= 1.49$, $p = 0.22$; Appendix S1: Table S7). Marine annelids accounted for on average 63% of the
422 infauna biomass in *G. vermiculophylla* mudflat sediment cores and 60% in bare mudflat cores
423 (Appendix S1: Table S7). When assessing small epibenthic invertebrate biomass separately in
424 the infaunal sediment cores, gastropods composed over 90% of the small epibenthos found in
425 each habitat type (Appendix S1: Table S7).

426 *Intermediate Scale Habitat Selection - Experimental Removal and Addition of Seaweed*

427 During the removal experiment, shorebirds on average foraged at a faster rate in 200 m²
428 plots with *G. vermiculophylla* than in plots with *G. vermiculophylla* removed (LMM: $\chi^2_1 = 4.18$,
429 $p = 0.04$, $n = 68$; Appendix S1: Fig. S1a). Yet shorebirds spent similar time (seconds) in each

430 treatment (GLMM: $\chi^2_1 = 2.23$, $p = 0.14$). For the two most common birds, dunlin foraged at
431 significantly faster rates where *G. vermiculophylla* was intact (LMM: $\chi^2_1 = 13.87$, $p < 0.01$, $n =$
432 24), while semipalmated plovers foraged at similar rates between treatments (LM: $F_{1,13} = 1.58$, p
433 $= 0.23$, $n = 15$; Appendix S1: Fig. S2a). We found no difference in the amount of time spent in
434 each treatment for either species (GLMM: $\chi^2_1 = 0.78$, $p = 0.38$; GLM: $\chi^2_1 = 2.58$, $p = 0.11$,
435 respectively).

436 In the addition experiment, we did not detect a difference in foraging rate in 200 m² plots
437 with or without *G. vermiculophylla* when all shorebirds were pooled (LMM: $\chi^2_1 < 0.01$, $p = 0.92$,
438 $n = 92$; Appendix S1: Fig. S1b); however, pooled shorebirds tended to spend more time in *G.*
439 *vermiculophylla* plots (GLMM: $\chi^2_1 = 3.07$, $p = 0.08$). Dunlin showed no difference in foraging
440 rate between treatments (LMM: $\chi^2_1 = 0.9$, $p = 0.34$, $n = 35$; Appendix S1: Fig. S2b). Dunlin also
441 spent similar amounts of time among treatments (GLMM: $\chi^2_1 = 0.09$, $p = 0.77$). Semipalmated
442 plovers again did not forage at different rates in bare mud versus *G. vermiculophylla* addition
443 plots (LM: $F_{1,21} = 2.02$, $p = 0.17$, $n = 23$; Appendix S1: Fig. S2b); yet, they spent more time in *G.*
444 *vermiculophylla* plots (GLM: $\chi^2_1 = 18.10$, $p < 0.01$).

445 *Patch Scale Foraging Behavior Study*

446 At the small scale (<1 m²), shorebird species differed in their foraging responses to *G.*
447 *vermiculophylla* patches. Dunlin ($n = 24$) weakly preferred *G. vermiculophylla* patches at the
448 population level, though individual preference varied (Fig. 2a; Appendix S1: Table S8). Least
449 sandpipers (a species that was pooled with other peeps at the large scale, $n = 15$) and ruddy
450 turnstones ($n = 5$) showed strong preferences for foraging in *G. vermiculophylla* patches at both
451 the individual and population level (Fig. 2b and 2d; Appendix S1: Table S8). In contrast, the
452 remaining peeps ($n = 7$) and semipalmated plovers ($n = 19$) avoided *G. vermiculophylla* patches
453 (Fig. 2c and 2e; Appendix S1: Table S8). Both willets ($n = 6$) and short-billed dowitchers ($n = 9$)
454 showed no overall preference for pecking in bare mud versus in *G. vermiculophylla* patches (Fig.
455 2f and 2g, respectively; Appendix S1: Table S8). However, individuals of both species varied
456 substantially, with some individuals preferring to forage in bare mud or *G. vermiculophylla*.

457 **Discussion**

458 Shorebirds demonstrated varied preferences for foraging habitat type across species and
459 spatial scales, suggesting complex mixed responses to the invasive ecosystem engineer, *G.*
460 *vermiculophylla* (see Table 1 for summary). Shorebird species were more abundant on large (>1

461 ha) mudflats with *G. vermiculophylla* relative to those without *G. vermiculophylla*, though the
462 strength of this density effect was clearly species dependent (Fig. 1; Appendix S1: Table S2). At
463 smaller spatial scales, the responses of birds to local patches of *G. vermiculophylla* depended on
464 species-specific foraging strategies (Fig. 2). Given that introduced ecosystem engineers can have
465 both positive and negative effects on communities (e.g. Boughton and Boughton 2014), the
466 varied responses of these community members suggest that behavioral mechanisms may help to
467 explain mixed effects of engineering, specifically in the context of novel habitat generation.

468 For ruddy turnstones, preference for mudflats with *G. vermiculophylla* at large spatial
469 scales (>1 ha) generally reflected foraging preferences at the small, patch-level scale (<1 m²) and
470 existing literature on their tendency to forage near structure. Ruddy turnstones typically use
471 structure to their advantage, turning over shell, stones and vegetation to reveal sheltering marine
472 invertebrates and eggs in dense aggregations (Fleischer 1983; Sullivan 1986; Nettleship 2000).
473 This behavior may pre-adapt the birds to readily utilize novel structure, such as that provided by
474 *G. vermiculophylla*. In Wassaw Sound, we often observed ruddy turnstones traveling from patch
475 to patch of *G. vermiculophylla*, flipping the seaweed over with their heads or beaks and picking
476 out epifaunal prey, including amphipods and crabs. Black-bellied plovers, a similarly sized
477 species that also forages visually and targets large epifaunal/epibenthic prey (Poole et al. 2016),
478 showed similar habitat selection at the large scale (>1 ha). Because of low densities, we could
479 not statistically assess their behavioral responses at smaller spatial scales (<1 m²).

480 Willets, short-billed dowitchers, and dunlin had greater densities on mudflats with *G.*
481 *vermiculophylla*, with varying effects of sediment composition and infauna densities on bird
482 densities (Appendix S1: Table S2). However, these species did not differ in foraging preferences
483 between bare mud and *G. vermiculophylla* patches at the smallest spatial scale (<1 m²), although
484 preference for *G. vermiculophylla* patches was statistically marginal for dunlin. These are larger
485 shorebirds, with long beaks used for tactile foraging, that often probe deep into the substrate to
486 capture infaunal prey, though willets and dunlin also use visual detection (Stenzel et al. 1976;
487 Rojas et al. 1999; Castillo-Guerrero et al. 2009; Novcic 2016). Given that these shorebirds forage
488 below the sediment surface, the presence of *G. vermiculophylla* may not hinder prey detection,
489 leading to their observed largely random foraging across patch types. This is further supported
490 by the lack of significant difference in infaunal prey densities and biomasses between sites in the
491 habitat preference survey (Appendix S1: Table S4-S7).

492 Semipalmated plovers and two peep species (western sandpipers and semipalmated
493 sandpipers) notably avoided foraging in *G. vermiculophylla* patches at the small scale (<1 m²),
494 but they either weakly preferred or had no preference for *G. vermiculophylla*-dominated
495 mudflats at the large scale (>1 ha). Avoidance of *G. vermiculophylla* patches by semipalmated
496 plovers emphasizes constraints of their foraging behaviors as this species relies heavily on visual
497 detection of infaunal polychaetes and other small epifaunal invertebrates (i.e., ostracods,
498 amphipods and small gastropods) (Rose et al. 2016). Such behavior suggests that *G.*
499 *vermiculophylla* presence may impede the plovers' prey detection, although they did not avoid
500 *G. vermiculophylla* mudflats at the large (>1 ha) or intermediate (200 m²) scales. Western and
501 semipalmated sandpipers predominantly rely on tactile detection of infaunal polychaetes and on
502 slurping of biofilm and small planktonic invertebrates (Nebel et al. 2005; Hicklin and Gratto-
503 Trevor 2010; Mathot et al. 2010). Thus, their greater densities on *G. vermiculophylla* mudflats,
504 but avoidance of small seaweed patches, may point to these birds cuing into other key factors at
505 the large scale, such as sediment composition (Appendix S1: Table S2, S3). Notably, the third
506 peep species, least sandpipers, strongly preferred foraging in *G. vermiculophylla* patches at the
507 small scale – a pattern distinct from the other peeps species. Indeed, least sandpipers are known
508 to utilize heavily vegetated microhabitats for foraging (Novcic 2016) and feed primarily on
509 amphipods (Nebel and Cooper 2008). Thus, peeps and semipalmated plovers provide notable
510 examples of how species identity (particularly morphology, behavior, and ecological niche) can
511 alter the overall response of a community to an invasive ecosystem engineer.

512 The results of the manipulative field experiments demonstrate the complexity of *G.*
513 *vermiculophylla*'s role in the observed mixed effects between the large and the small scale
514 studies. For instance, semipalmated plovers showed no difference in peck rate between
515 treatments in either experiment (Appendix S1: Fig. S2). The lack of response in foraging effort
516 by semipalmated plovers between treatments was expected given their lack of response to algal
517 presence in the Large Scale Habitat Selection Survey (>1 ha). Their indifference also indicates
518 that the presence of *G. vermiculophylla* may not negatively affect semipalmated plover foraging
519 effort, despite their avoidance of *G. vermiculophylla* patches at the small scale (<1 m²). On the
520 other hand, dunlin showed a mostly positive response to the alga. At the large scale (>1 ha),
521 dunlin densities were greater on *G. vermiculophylla* mudflats. Additionally, at the small scale
522 (<1 m²), dunlin showed a slight preference for foraging in *G. vermiculophylla* patches, with great

523 variability in foraging response between individuals. In the experiments, dunlin pecked at faster
524 rates where *G. vermiculophylla* was left intact; however, *G. vermiculophylla* had no effect on
525 dunlin foraging in the experiments where it was newly added to mudflats. Therefore, lower peck
526 rate in response to *G. vermiculophylla* removal may be the result of a covarying factor (i.e., prey
527 density or sediment characteristics) that is not expressed immediately upon the addition of *G.*
528 *vermiculophylla*. Despite the contrasting results between species, it is notable that across all the
529 experiments, observations and species, birds rarely preferred the native bare habitat relative to *G.*
530 *vermiculophylla* (Table 1). Thus, *G. vermiculophylla* seems to generate either no or a positive
531 response by shorebirds, though the mechanism is likely different for each species examined.

532 The presence of contrasting preferences at the large scale (>1 ha) and small scale (<1 m²)
533 may indicate the importance of other habitat variables that may simultaneously affect shorebird
534 densities and *G. vermiculophylla* presence. For dunlin, short-billed dowitchers, willets and peeps,
535 some variation in densities depended on sediment composition and/or infaunal densities in the
536 Large Scale Habitat Selection Survey. Additionally, *G. vermiculophylla* presence on
537 southeastern mudflats is tightly correlated with the density of native tubeworms, *D. cuprea*,
538 which attaches the seaweed to its tube (Byers et al. 2012; Kollars et al. 2016). *D. cuprea*
539 densities are dependent on abiotic conditions, such as salinity, sediment type, and inundation
540 (Berke 2012; Kollars et al. 2016), and thus restrict *G. vermiculophylla* distributions to the lower
541 estuary even though *G. vermiculophylla* can tolerate the lower salinities of the upper estuaries
542 (Weinberger et al. 2008; Sotka et al. 2018). Beyond habitat characteristics, the mixed effects of
543 *G. vermiculophylla* on shorebird habitat selection and foraging behavior across spatial scales
544 could be partially attributable to flocking behavior, whereby birds following the cues of other
545 species or individuals may be led to less preferred foraging habitat.

546 Although shorebirds generally responded positively to the invasive ecosystem engineer's
547 presence at the large scale (>1 ha), their responses at the small scale (<1 m²) were mixed, despite
548 the increased epifaunal prey availability within *G. vermiculophylla* patches (Byers et al. 2012;
549 Wright et al. 2014). The divergent bird responses demonstrate that even polyphagous predators
550 within the same trophic assemblage experience effects of biological invasions differently.
551 Though our methods cannot address the invasive engineer's impact on shorebird fitness, our
552 results do indicate that invasive ecosystem engineers that provision additional complex habitat
553 and boost associated prey abundance do not positively affect all native species, even those that

554 utilize similar prey resources. Rather, predators utilize these new habitats differently across
555 spatial scales based on inherent foraging behaviors. Thus, as invasive ecosystem engineers
556 become more prevalent globally, the direction of their local effects may depend in part on
557 species-specific behaviors.

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760 Table 1. Summary of habitat associations and preferences determined from surveys, experiments,
761 and behavioral studies for the common shorebird species examined. Two plus signs (++) indicate
762 a statistically significant positive relationship between *G. vermiculophylla* presence and bird
763 density or foraging, while one (+) indicates a positive trend ($0.05 < p < 0.1$). An equal sign (=)
764 indicates no difference between treatments. **B** indicates a significant preference for bare mudflat.
765 Foraging ecology was determined from literature reviews, with individual species reviews from

766 *The Birds of North America* (Rodewald 2015) as important sources. We merged three peep
 767 species for the Large Scale Habitat Selection Survey due to identification limitations; during the
 768 Patch Foraging Preference study, least sandpipers were identifiable, while western and
 769 semipalmated sandpipers were pooled. Dashes indicate no analysis due to species absence.

Shorebird Species	Foraging Ecology Visual, Tactile, or Mixed	Habitat Selection Surveys (>1 ha)	<i>Gracilaria</i> Removal Foraging (200 m ²)	<i>Gracilaria</i> Addition Foraging (200 m ²)	Patch Foraging Preference (<1 m ²)
Dunlin (<i>Calidris alpina</i>)	Tactile (Mixed)	+ +	+ +	=	+
Western Sandpiper (<i>Calidris mauri</i>)	Mixed	+	---	---	B
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	Mixed		---	---	
Least Sandpiper (<i>Calidris minutilla</i>)	Visual (Mixed)	+	---	---	+ +
Ruddy Turnstone (<i>Arenaria interpres</i>)	Visual	+	---	---	+ +
Black-Bellied Plover (<i>Pluvialis squatarola</i>)	Visual	+ +	---	---	---
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	Visual	=	=	=	B
Willet (<i>Tringa semipalmata</i>)	Tactile (Mixed)	+ +	---	---	=
Short-Billed Dowitcher (<i>Limnodromus griseus</i>)	Tactile	+ +	---	---	=

770
 771 Figure 1. Field surveys of shorebird density (shorebirds/ha) on twelve mudflats (six with
 772 *Gracilaria* and six with no *Gracilaria*, or “bare”) for (a) all birds and (b-h) individual species.
 773 Data were analyzed after natural log-transformation using linear regression in R (3.3.2). Figures
 774 depict raw densities from the algal presence-only model. * indicates a trend (0.05 < p > 0.1) and
 775 ** indicates significant difference (p ≤ 0.05). Species are presented as follows: b) dunlin; c)
 776 peep; d) ruddy turnstone; e) black-bellied plover; f) semipalmated plover; g) willet; and h) short-
 777 billed dowitcher. Illustration credit: Rebecca Atkins

778 Figure 2. Foraging-habitat patch preferences for shorebirds during the 2015 spring migration
779 season. We analyzed all species for individual-level (dotted lines) and population-level (solid
780 lines) preferences using a hierarchical Bayesian analysis in R (3.3.2). Preference curves for *G.*
781 *vermiculophylla* patches is illustrated in red and for bare mud in blue. Arrows denote where the
782 preference curves should peak for each patch type if the birds foraged randomly, given the
783 average percent cover of each habitat patch type. Filled arrows indicate that birds foraged
784 differently from the random distribution, while unfilled arrows indicate that birds foraged
785 randomly. Lightly filled arrows in panel b indicate a marginal difference from random foraging
786 (credible intervals slightly overlap with patch-type cover). Species are presented as follows: a)
787 dunlin (n = 24); b) least sandpiper (n = 15); c) peep (n = 7); d) ruddy turnstone (n = 5); e)
788 semipalmated plover (n = 19); f) willet (n = 6); g) short-billed dowitcher (n = 9). Illustration
789 credit: Rebecca Atkins

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