

Swarms of swift scavengers:
ecological role of marine intertidal hermit crabs in California

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1 **Abstract**

2 While marine hermit crabs are well known for being omnivorous filter feeders, less is
3 known about the role they may play as active carrion scavengers in intertidal ecosystems.
4 Prior studies have revealed that intertidal hermit crabs can be attracted to chemical cues
5 from predated gastropods. Yet their attraction is usually assumed to be driven primarily
6 by the availability of new shells rather than by food. We conducted field experiments to
7 assess hermit crabs' potential role as generalist carrion scavengers on the California
8 coast, examining their speed of attraction and the size of the aggregations they formed in
9 response to chemical cues from freshly smashed gastropods and mussels, both of which
10 indicated available carrion. Compared to all other marine species, hermit crabs (including
11 *Pagurus samuelis*, *Pagurus hirsutiusculus*, and *Pagurus granosimanus*) were the fastest
12 to arrive at the provisioning sites, and they also dominated the provisioning sites, forming
13 aggregations of up to 20 individuals, which outcompeted all other scavengers for carrion.
14 Notably, hermit crabs arrived equally quickly for both smashed gastropod and mussel,
15 even though the latter does not offer suitable shells for hermit crabs and even though the
16 former only yields shell-related chemical cues over time frames longer than our
17 experiments. These results thus suggest that shell availability is not the only, or even the
18 primary, reason marine intertidal hermit crabs aggregate at carrion sites; they also
19 aggregate to forage, thereby playing an important role as active carrion scavengers in
20 intertidal ecosystems.

21

22 **Keywords:** chemical ecology; field provisioning experiments; hermit crabs; rocky
23 intertidal; tide pools; scavengers

24

25 **Introduction**

26 Tide pools within the rocky intertidal boast exceptionally high levels of
27 biodiversity as well as some of the strongest levels of physical disturbance of any habitat
28 (Denny and Gaines 2007). Ocean waves crashing on rocky shores routinely move at
29 speeds of more than 5 m/s (Gaylord 1999), generating powerful hydrodynamic forces that
30 can dislodge even well anchored organisms (Denny et al. 1998; Gaylord et al. 2001).
31 Intertidal wave action can also shift rocks and other heavy materials, putting organisms at
32 risk of being smashed in spite of their protective shells and armored exteriors (Vermeij
33 1993). As a consequence, carrion is frequently produced in tide pools within the rocky
34 intertidal, both through abiotic forces like wave action and through biotic forces like
35 shell-crushing predators (Vermeij 1993). Many species rely on such carrion ‘casualties’
36 and the trophic transfer of nutrients they provide (King et al. 2007). However, the
37 availability of fresh carrion is unpredictable (Britton and Morton 1994) and therefore the
38 most effective scavengers must be able to quickly locate and dominate new carrion
39 resources. What species show such behavioral specializations for a scavenging lifestyle in
40 tide pools?

41 Of the many organisms that inhabit tide pools, crustaceans exhibit acute
42 chemosensory abilities (reviewed in Breithaupt and Theil 2011). As such, many
43 crustaceans can quickly locate the scent of carrion and orient to this valuable food source.
44 As crustaceans, hermit crabs (Decapoda, Anomura) share these fine chemosensory
45 abilities (Gherardi and Tricarico 2011), and their mobility and abundance in tide pools
46 makes them excellent candidates as carrion scavengers (Britton and Morton 1994).
47 Intertidal hermit crabs, however, are primarily considered microphagous detritivores

48 (Reese 1969; Kunze and Anderson 1979; Hazlett 1981; Rittschof 2007) and are thought
49 to only scavenge for carrion as a secondary foraging strategy (Schembri 1982). Yet
50 surprisingly little empirical work has actually assessed hermit crab's effectiveness as
51 carrion scavengers or compared them with other sympatric intertidal species. Indeed, as
52 Hazlett (1981, p. 1) noted on the first page of his review of hermit crab behavior, still
53 authoritative after over three decades: "Most ecological studies have focused completely
54 on the crab-shell interaction, and relatively little work has been done on the crabs as an
55 element of marine ecosystems." Consequently, relatively little is known about the feeding
56 ecology of many intertidal hermit crabs (Bertness 1981; Hazlett 1981; Elwood and Neil
57 1992; Tran 2013), so their potential role as active scavengers in intertidal ecosystems has
58 not been fully addressed.

59 Pioneering experiments by McLean (1974) and Rittschof (1980a) highlighted
60 hermit crabs' attraction to simulated predation sites involving the scent of killed
61 gastropods. An ability to quickly locate gastropod predation events may aid hermit crabs
62 in finding new shells, since many predators leave shells intact after consuming the
63 gastropod's flesh (reviewed in Table 1 of McGuire and Williams 2010). It has therefore
64 been argued (Rittschof 1980b, 1992; Rittschof et al. 1992; Mclean 1983; Gilchrist 1984;
65 Pezzuti et al. 2002; Tricarico and Gherardi 2006; Tricarico et al. 2009) that hermit crabs
66 are attracted to the scent of gastropod flesh primarily, if not exclusively, because it serves
67 as an indicator of shell availability. Critically though the attractants in gastropod flesh
68 that indicate shell availability are only released an hour or more after a gastropod is
69 smashed; or if the gastropod flesh is treated with predator proteases like trypsin, which
70 generates small peptides that serve as 'shell cues' (Rittschof 1980b). In contrast, carrion

71 from freshly smashed gastropod that is less than 1 h old and has not been treated with
72 proteases (or carrion from non-gastropod sources) should only be attractive to hermit
73 crabs as food, given it does not provide shell-related cues. So hermit crabs attracted to
74 such non-shell carrion?

75 Interestingly, laboratory studies have demonstrated that despite the absence of
76 shell cues, fresh gastropod carrion as well as other types of non-gastropod carrion can
77 sometimes be attractive to hermit crabs (Tricarico et al. 2011). Additionally, both
78 laboratory and field observations have suggested that even when crabs are attracted to
79 carrion from gastropods, they may show an interest not just in entering a new shell but
80 also in consuming the flesh remaining within the shell (Laidre 2011; McGuire and
81 Williams 2010). Notably, some predators do not leave gastropod shells intact or suitable
82 for occupation by hermit crabs (Vermeij 1993), even though a by-product of their
83 predation may be strong chemical ‘shell cues’ indicative of gastropod death. Thus, even
84 the scent of gastropod flesh that is more than an hour old will not always be predictive of
85 newly available shells. And yet hermit crabs might still benefit from being attracted,
86 given the value of carrion itself as a protein-rich food source worth fighting over (Britton
87 and Morton 1994; Laidre 2007). Hermit crabs might therefore fulfill an important
88 ecological role within marine ecosystems if their scavenging extends beyond searching
89 for shells. Is there any evidence that hermit crabs fulfil such a generalist foraging role?

90 In the laboratory, hermit crabs signal and fight intensely for mussel (Laidre 2007;
91 Laidre and Elwood 2008), a carrion source that is not associated with a suitable shell
92 home for hermit crabs. And in the wild, a limited number of field experiments have
93 suggested that hermit crabs can be highly motivated for other non-gastropod carrion.

94 Specifically, Ramsay et al. (1997) deployed an underwater video camera to film
95 scavengers that were experimentally attracted to dead fish bait dropped into the sub-tidal.
96 Only two trials were conducted, but in both trials hermit crabs (*Pagurus bernhardus*)
97 were the fastest scavengers to arrive at the site, forming the largest aggregations of any
98 species, and remaining at the site for extended periods to fight for and feed on the carrion.
99 Similarly, Scully (1983) reported a single trial involving a crushed mussel in the intertidal
100 and found that nearly 100 hermit crabs (*Pagurus longicarpus*) swiftly swarmed to and
101 dominated the site within minutes. Both these preliminary reports deserve more
102 systematic follow-ups, with a larger number of trials.

103 Here we examined the potential role of hermit crabs as scavengers based on their
104 attraction to fresh carrion that lacked any associated ‘shell cues’. Our experiments tested
105 the attractive value of two types of carrion, gastropod and mussel carrion. Mussel does
106 not provide a suitable shell for hermit crabs, so when smashed it should be attractive only
107 as an eatable carrion source. Likewise, because we provided both the mussel and the
108 gastropod carrion immediately after smashing live specimens, we ensured that there were
109 no shell cues associated with the gastropod carrion. Our experiments thus revealed how
110 strongly hermit crabs were attracted to carrion that was purely indicative of food rather
111 than shells. We incorporated controls for each carrion type and structured our
112 observations to reveal the total number of crabs that aggregated (the size of their
113 ‘swarm’) as well as the temporal dynamics over which they were attracted (how ‘swiftly’
114 they arrived). Moreover, we compared hermit crabs’ attraction to the carrion with that of
115 sympatric species to measure hermit crabs’ relative importance as scavengers within the
116 ecosystem. Our experiments therefore allowed us to ask whether intertidal hermit crabs

117 perform an important ecological role, acting as swarms of swift scavengers that converge
118 to feed on intertidal carrion more quickly and in greater abundance than other species.

119

120 **Methods**

121 Study site and species

122 We conducted our experiments in the Pacific intertidal off the coast of California,
123 an area renowned for its biodiversity (Morris et al. 1980). Prior field experiments on
124 hermit crabs' attraction to simulated predation sites have, for the most part, been
125 conducted in the Atlantic Ocean (Rittschof 1980a; Tricarico and Gherardi 2006) and the
126 Mediterranean Sea (Tricarico et al. 2009), so our study provides valuable comparative
127 data from the Pacific. Observations and experiments were carried out in the rocky
128 intertidal habitat (Figure S1) outside the Bodega Marine Laboratory, located on the
129 Bodega Marine Reserve in Sonoma County. A rich community of marine species inhabits
130 this area of the intertidal, including: (1) three species of hermit crabs (*Pagurus samuelis*,
131 *Pagurus hirsutiusculus*, and *Pagurus granosimanus*; Bollay 1964); (2) a variety of
132 species of shelled mollusks, with the California mussel (*Mytilus californianus*) being
133 especially abundant, and with the black turban snail (*Chlorostoma funebrate*, previously
134 classified as *Tegula funebris*) being the most abundant gastropod; (3) many species of
135 brachyuran crabs (including members of the *Pugettia*, *Scyra*, *Cancer*, *Lophopanopeus*,
136 *Pachygrapsus*, and *Hemigrapsus* genera); and (4) several species of gobie (Gobiidae)
137 (Morris et al. 1980). Carrion produced in this area of the intertidal is thus potentially
138 available to many species.

139

140 General experimental protocol

141 To investigate hermit crab carrion scavenging we conducted 100 experiments, 80
142 described in this section and another 20 described in the next section. For 80 experiments
143 we provisioned tide pools with either a gastropod (*C. funebrale*) or a mussel (*M.*
144 *californianus*). Of these 80 experiments, 20 each were conducted using (i) a live
145 gastropod (control), (ii) a gastropod killed by smashing, (iii) a live mussel (control), or
146 (iv) a mussel killed by smashing. Local rocks were used to smash the gastropods and
147 mussels. All experiments were conducted during daylight at low tide, spanning February
148 to July 2011. The experimental condition (gastropod or mussel, live or smashed) was
149 randomly allocated.

150 Each experiment involved the same core design and set of steps. First the
151 experimenter (either A.G. or M.L.) located a tide pool. Most tide pools at the study site
152 have lengths and widths between one and three meters. We found a flat area within the
153 tide pool that was open to observation and not obscured by seaweed. We then set down a
154 quadrat (14.5 x 14.5 cm) composed of black wire. This quadrat was used to demarcate the
155 focal area immediately surrounding where the stimulus (gastropod or mussel) was
156 eventually introduced. After placing the quadrat, the experimenter moved to the edge of
157 the tide pool and observed for several minutes to confirm that hermit crabs were present
158 within the pool. If there was at least one hermit crab on two or more sides of the quadrat,
159 then the experimenter remained in position and began an experiment (Figure 1).
160 Throughout the experiment the experimenter remained stationary while observing the
161 quadrat from above.

162 Each experiment lasted 20 min, the design paralleling experiments in terrestrial
163 hermit crabs by Laidre (2010). During the first 10 min (from $t = -10$ to $t = 0$ min) we
164 collected baseline data on the number of hermit crabs and any other macroscopic
165 scavengers (gastropods, brachyuran crabs, and gobies) that we observed in the quadrat at
166 1-min intervals. During this control period no materials had yet been placed inside the
167 quadrat, so the data indicate the general background activity within the tide pools. At the
168 end of the control period ($t = 0$ min), the experimenter extended his or her arm above the
169 quadrat and dropped a set of prepared materials (detailed below) into the center of the
170 quadrat. This arm movement and the materials that were dropped in typically caused
171 nearby hermit crabs to temporarily duck in their shells, but only temporarily. Usually
172 within seconds, crabs and other organisms emerged and resumed their prior behavior.
173 Once the materials had been dropped into the quadrat, initiating the experimental period,
174 we recorded the same data (on the number of crabs and other species present in the
175 quadrat) for another 10 min (from $t = 1$ to $t = +10$ min) at 1-min intervals. We noted the
176 exact time (to the nearest second) that an organism (hermit crab or other) first initiated
177 contact with the dropped in item. If the organism that first made contact was not a hermit
178 crab, then we also noted when the first hermit crab subsequently made contact with the
179 item. Since it was not possible to readily differentiate the three hermit crab species from
180 overhead (and all were present in the quadrats at the end of our experiments on multiple
181 occasions), we grouped them together in our count.

182 The materials that were dropped into the quadrat (gastropod or mussel, whether
183 live or smashed) were wrapped in black rubber mesh that was tied with thin wire and
184 weighted down with a metal weight (100 g). The mesh allowed carrion chemical cues to

185 emanate and also allowed scavengers to pick at available carrion while still keeping the
186 specimen (whether live or smashed) consolidated. The metal weight anchored the
187 materials inside the quadrat, so that attraction to the bait could be readily observed. We
188 collected the mussel or gastropod specimen immediately prior to each experiment,
189 preparing the materials to be dropped in during the 10 min control period and then
190 smashing the specimen (if it was to be killed) immediately before $t = 0$ min. Mussel and
191 gastropod specimens were chosen such that the raw amount of flesh they contained was
192 approximately equal: the mussels, with their elliptical shape, were chosen with lengths of
193 2-3 cm, while the gastropods, with their more globular shape, were chosen with lengths
194 and heights of 1-2 cm.

195 At the end of each experiment, the quadrat, the attached weight, and the
196 experimenter's hands were all washed thoroughly in seawater before beginning the next
197 experiment, thus eliminating any residual odor from the prior experiment. New mesh and
198 new wire were used for each experiment. Individual tide pools were only tested once per
199 day, and on subsequent test days we targeted our experiments in different broad sections
200 of our study site (see Figure S1) to avoid re-testing the same tide pools. In the few cases
201 where some tide pools might possibly have been re-tested, there were at least several
202 days (and up to 30 days) intervening since they were last tested—and thus the highly
203 mobile inhabitants in these pools, like hermit crabs, had almost certainly changed.

204

205 Extended experiments

206 An additional set of 20 extended experiments were conducted using the same core
207 design as described above, with a lengthened experimental period that lasted for 30 min

208 after the materials were dropped into the tide pool. These experiments all used smashed
209 mussel, and were undertaken to determine if the number or composition of scavengers
210 inside the quadrat varied over longer periods.

211

212 Analyses and predictions

213 We tested the effect of each of the four conditions (gastropod smashed, gastropod live,
214 mussel smashed, and mussel live) on the number of hermit crabs and other attendants
215 attracted to the quadrat and on the speed with which contact was first made. All data
216 analyses were conducted in R (R Core Team 2012). For data that was non-normally
217 distributed, we first tried transforming the data and otherwise used non-parametric tests.

218 We predicted that if eatable, non-shell carrion is attractive to hermit crabs, then
219 the number of hermit crabs within the quadrat would significantly increase from the
220 control period to the experimental period in both the gastropod smashed and mussel
221 smashed conditions, but not in the two control conditions (gastropod live and mussel
222 live). To test this prediction we compared the final sample point during the control period
223 ($t = 0$ min) with the final sample point during the experimental period ($t = +10$ min). The
224 means for each of these sample points, across all experiments of a given condition, were
225 compared using a Wilcoxon signed rank test (a non-parametric equivalent to a paired t-
226 test, since data were not always normally distributed). We also conducted a separate
227 analysis in which we compared (1) the average number of crabs in the quadrat during the
228 10 sample points in the control period ($t = -10$ to $t = -1$ min) with (2) the average number
229 of crabs in the quadrat during the 10 sample points in the experimental period ($t = +1$ to t
230 $= +10$ min). The ten counts made during each of these two periods were then averaged

231 and the means across all experiments were compared with a Wilcoxon signed rank test.
232 Ultimately, we obtained similar results from both these different analyses, aside from one
233 exception. In the Results section we therefore report the one exception and otherwise
234 only detail our analyses based on comparing the final two sample points.

235 If both gastropod and mussel carrion in general is attractive to hermit crabs, then
236 we predicted there would be no significant difference between the gastropod smashed
237 condition and the mussel smashed condition, either in the number of hermit crabs that
238 accumulated in the quadrat or in the speed with which hermit crabs first arrived and
239 contacted each type of carrion. We tested this prediction by examining the number of
240 hermit crabs in the final sample point ($t = +10$ min) for the gastropod smashed and
241 mussel smashed conditions and by examining when hermit crabs first touched each type
242 of carrion.

243 All the tests described above were also carried out for every species besides
244 hermit crabs that was counted inside the quadrat. We predicted that if hermit crabs fulfill
245 an important scavenging role compared to other organisms in the intertidal, then hermit
246 crabs would show a significant increase in response to carrion whereas other organisms
247 would not. We also predicted that if hermit crabs are not just scavengers but are also
248 swift scavengers, then they would consistently be the first organism to make contact with
249 the carrion after it was dropped into the quadrat.

250 Finally, to test whether the number or composition of scavengers varied over
251 longer time periods, we compared the scavengers present in the quadrat at the end of the
252 normal-length experiments ($t = +10$ min) versus the end of the longer experiments ($t =$
253 $+30$ min), both of which involved smashed mussel.

254 Figures in the results show the counts of hermit crabs made at each 1-min sample
255 point across the entire experiment (from $t = -10$ to $t = +10$ min), documenting the
256 temporal dynamics of hermit crabs' numbers within the quadrat.

257

258 **Results**

259 Increase in hermit crab numbers

260 Hermit crabs were strongly attracted to the carrion in the gastropod smashed and
261 mussel smashed conditions, with their numbers rising steeply across the experimental
262 period (Figure 2). In particular, hermit crabs increased significantly in the quadrat
263 between the end of the control period and the end of the experimental period for both
264 conditions (Wilcoxon signed-rank tests; smashed gastropod: $T = 3$, $N = 20$, $p < 0.0001$;
265 smashed mussel: $T = 4$, $N = 20$, $p < 0.0001$; effect sizes for both conditions were large:
266 Table 1). No such increase in the number of hermit crabs occurred for either the
267 gastropod live or the mussel live condition (Wilcoxon signed-rank test; gastropod live: T
268 $= 102$, $N = 20$, $p = 0.874$; mussel live: $T = 75$, $N = 20$, $p = 0.312$)¹. In addition to
269 accumulating in number within the quadrat, hermit crabs were also significantly more
270 likely to contact the smashed gastropod and mussel conditions compared to the live
271 gastropod and mussel conditions (Fisher's exact test: $p < 0.001$; Figure 3A).

272

273 Attraction to gastropod versus mussel

274 The smashed gastropod and mussel conditions appeared equally attractive to
275 hermit crabs: there was no difference between these conditions in the number of hermit

¹ In the mussel live condition, there was a significant (but minor) increase in the number of hermit crabs between the control and experimental period: this occurred only when the analysis included all sample points, rather than just the two at the end of the control and experimental period (compare Tables 1 and 2).

276 crabs that accumulated at the end of the experimental period (Mann-Whitney U test; U=
277 19.93, $N_1 = 20$, $N_2 = 20$ $p = 0.604$; compare Figure 2A versus 2C). Nor was there a
278 difference in the speed with which hermit crabs first made contact with either type of
279 carrion (data log transformed, t-test; $t_{35} = 0.1367$, $p = 0.89$; Figure 3B).

280

281 Hermit crabs versus other organisms

282 In contrast to the results for hermit crabs, no other organisms showed a significant
283 change in abundance between the control and experimental period for any of the
284 conditions (Table 1; Figures S2-S4). Moreover, hermit crabs were consistently the first
285 organism to make contact with both the gastropod and the mussel, whether it was
286 provided smashed or live: of our $N = 80$ experiments, in $N = 58$ experiments an organism
287 successfully contacted the item within 10 min of our dropping it in, and in all but one of
288 those instances the organism making first contact was a hermit crab.

289

290 Aggregation size over time

291 The size of hermit crabs' aggregations did not change when they were given three
292 times longer to aggregate: no significant difference existed in the number of hermit crabs
293 10 min after compared to 30 min after the smashed mussel was dropped-in (Mann-
294 Whitney U test: $U = 32.34$, $p = 0.395$; Figure 4). Hermit crabs thus reached peak
295 aggregation size relatively quickly in response to carrion.

296

297 **Discussion**

298 Shells represent an important resource for hermit crabs' reproductive success
299 (Hazlett 1981). However, shells are not the only resource that matters for hermit crabs
300 (Schembri 1982; Ramsay et al. 1997; Laidre 2011; Tran 2013; Tran et al. in press). Like
301 other organisms, hermit crabs must acquire enough food to fuel growth and survival.
302 Carrion may, therefore, represent a critical food resource for hermit crabs, especially in
303 the intertidal, where high levels of abiotic and biotic disturbance frequently result in
304 organisms either being smashed by waves (Denny et al. 1998; Gaylord 1999, 2007;
305 Gaylord et al. 2001) or crushed by predators (Vermeij 1987, 1993).

306 In the present study, we simulated carrion production in the intertidal by smashing
307 shell-bearing organisms (gastropods and mussel) that live sympatrically with hermit
308 crabs. We found that hermit crabs were strongly attracted to this carrion, even though
309 neither carrion source was associated with shell cues and thus only indicated a potential
310 food resource. Our results thus suggest that marine intertidal hermit crabs are not solely
311 attracted to scents that indicate shell availability and that, at least in some populations,
312 hermit crabs are highly motivated for carrion consumption (Scully 1983; Ramsay et al.
313 1997)². These results contrast with some other studies that have provisioned carrion to
314 hermit crabs (e.g., Rittschof 1980a, Gilchrist 1984; Bozzano and Sarda 2002), which
315 found that hermit crabs are only attracted to gastropod carrion once it begins to emanate
316 peptides that are shell cues. What could account for these divergent results?

317 Different populations of hermit crabs may experience varying degrees of food
318 versus shell limitation, with some areas having a more reliable supply of food and some
319 having a more reliable supply of shells (Hazlett 1981; Barnes and De Grave 2000).

² Similar attraction to smashed mussel and other carrion occurs in intertidal hermit crabs in Northern Ireland (*Pagurus bernhardus*) and in Costa Rica (*Clibanarius albidigitus* and *Calcinus obscurus*) (Laidre, personal observation).

320 Spatial heterogeneity in food or shell availability could therefore account for the
321 differences between studies that have examined hermit crabs' motivation for carrion with
322 versus without shell cues. Interestingly, even within the same population, hermit crabs'
323 relative motivation for edible carrion versus carrion that is also indicative of shells could
324 change dramatically across time due to large-scale ecological events, like red tides
325 (Prezelin 2007). Such events may kill vast numbers of gastropods, while leaving their
326 shells intact, thereby generating a temporarily surplus of shells in the hermit crab housing
327 market and increasing the importance of carrion as a source of food to fuel growth.
328 Additionally, if crabs are satiated before being offered chemical cues (e.g. Gherardi and
329 Atema 2005), then their attraction to food related cues would likely lessen. Further
330 comparative studies across hermit crabs species, as well as studies focusing on single
331 hermit crab populations during temporally dynamic ecological events, could reveal
332 interesting switch points in crabs' relative resource motivation. A fundamental predictor
333 should be which resource (shells or food) is currently most limiting in the population: at
334 sites where hermit crabs have few shells, they should be more attracted to carrion associated
335 with shell cues; whereas at sites where hermit crabs have abundant shells but limited food
336 they should be attracted to carrion even if it lacks shell cues.

337 While hermit crabs aggregated quickly for carrion in our study and while these
338 aggregations persisted across time, the precise behaviors that crabs exhibited within their
339 aggregations could not be quantified under the field conditions of our experiments. We
340 did consistently observe hermit crabs feeding on both forms of carrion (gastropod and
341 mussel) by picking through the mesh and eating bits of torn flesh. However, it was
342 unclear whether crabs might have also exhibited some behaviors related to shell

343 acquisition (e.g., by fighting or ‘piggybacking’ on each other’s shells in anticipation of a
344 shell switch). Such behaviors are possible because even if crabs are originally attracted to
345 a site for the purpose of eating, other motivations could subsequently surface. Controlled
346 laboratory experiments (e.g., Tricarico et al. 2011) would enable greater focus on crabs’
347 fine-grained behavior within aggregations.

348 Even if hermit crabs may be motivated to eat carrion, the question remains how
349 their carrion scavenging compares with other scavenging species in the ecosystem
350 (Britton and Morton 1994; King et al. 2007; Breithaupt and Theil 2011). Our study
351 suggests that hermit crabs can be swarms of swift scavengers, performing an essential
352 carrion scavenging role in intertidal ecosystems: hermit crabs were consistently the
353 fastest to arrive at our sites, accumulated in the largest numbers, and their aggregations
354 persisted across extended time periods. These results, however, do not imply that hermit
355 crabs are necessarily the most dominant scavenger at all times. All our experiments were
356 conducted at low tide, so it is possible that at high tide other species might outcompete
357 hermit crabs for carrion. Indeed, at high tide, fish and other larger scavengers might be
358 able to arrive at carrion sites faster than hermit crabs. Additionally, hermit crab behavior
359 may differ at high tide because the influx of large predators forces some hermit crab
360 species to take refuge in protective crevices (Bertness 1981). Only by conducting
361 identical experiments at high tide, perhaps using underwater cameras to record the
362 attracted scavengers, could the generality of hermit crabs’ scavenging dominance be
363 tested (though see Ramsay et al. 1997 for evidence of scavenging dominance in sub-tidal
364 hermit crabs). It is clear from studies in other areas (e.g., the sandy shores in Hong Kong:
365 Morton and Yuen 2000) that hermit crabs are not always the most dominant scavenger;

366 other sympatric species, such as carnivorous gastropods, can sometimes outcompete
367 them. Nevertheless, at rocky intertidal sites in California, hermit crabs appear to perform
368 a generalized scavenging role that, at low tide, outstrips any other sympatric species,
369 invertebrate or vertebrate.

370

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378

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Table 1 Wilcoxon signed rank tests comparing the number of each organism at the end of the control period (t = 0 min) versus the end of the experimental period (t = +10 min).

	<i>Experimental condition</i>			
	Gastropod smashed	Gastropod live	Mussel smashed	Mussel Live
Hermit Crabs	T = 3, p<0.0001, ES = 0.947	T = 102, p = 0.874	T = 4, p<0.0001, ES = 0.944	T = 75, p = 0.312
Gastropods	T = 87, p = 0.497	T = 96, p = 0.604	T = 77, p = 0.386	T = 89, p = 0.574
Brachyuran crabs	T = 104, p = 0.510	T = 105, p = 0.492	T = 96, p = 0.514	T = 96, p = 0.507
Gobies	T = 105, p = 0.566	T = 86, p = 0.465	T = 86, p = 0.500	T = 96, p = 0.559

N = 20 for each condition. To break ties and deal with zeroes in the data, we randomly altered counts by 0.001 in either direction. This process was repeated 1000 times and the average V statistic and p value reported. Effect sizes are listed where significant effects occurred.

Table 2 Wilcoxon signed rank tests comparing mean abundance across the entire control period (t = -10 to -1 min) versus the entire experimental period (t = +1 to +10 min).

	<i>Experimental condition</i>			
	Gastropod smashed	Gastropod live	Mussel smashed	Mussel Live
Hermit Crabs	T = 7, p<0.0001, ES = 0.887	T = 79, p = 0.340	T = 3, p<0.0001, ES = 0.970	T = 47, p = 0.030, ES= 0.42
Gastropods	T = 70, p = 0.286	T = 91, p = 0.621	T = 72, p = 0.285	T = 98, p = 0.759
Brachyuran crabs	T = 95, p = 0.514	T = 104, p = 0.522	T = 91, p = 0.499	T = 103, p = 0.512
Gobies	T = 93, p = 0.582	T = 79, p = 0.391	T = 88, p = 0.488	T = 88, p = 0.514

N = 20 for each condition. To break ties and deal with zeroes in the data, we randomly altered counts by adding small amounts of noise (around 0.001) in either direction. This process was repeated 1000 times and the average V statistic and p value reported. Effect sizes are listed where significant effects occurred.

Figure legends

Figure 1. (1) Conditions necessary for experiment to begin, with timeline below showing 10-min control period and (2) Time at which experimental stimulus was dropped in (at $t = 0$ min), with timeline below showing 10-min experimental period. Icons represent: (a) experimenter, (b) tide pool, (c) quadrat, (d) hermit crab, (e) mesh with experimental item, and (f) weight.

Figure 2. Number (Mean + SE) of hermit crabs present within the quadrat during each minute of the experiment. At $t = 0$ min the experimental stimulus was dropped into the tide pool. $N = 20$ trials for each condition: (a) gastropods that were smashed, (b) gastropods that were live, (c) mussels that were smashed, and (d) mussels that were live.

Figure 3. (a) Proportion of trials in which hermit crabs contacted the experimental stimulus ($N = 20$ trials for each condition). (b) Time (Mean + SE) till hermit crabs contacted the experimental stimulus (calculated from when the stimulus was dropped into the tide pool at $t = 0$ min). Note that since the stimulus was not contacted in every experiment, sample sizes differed across conditions (listed below each bar).

Figure 4. Number (Mean + SE) of hermit crabs that accumulated at 10 min versus 30 min after the mussel smashed condition.

Electronic Supplementary Material

Figure S1. Google Earth image of the intertidal study site outside the Bodega Marine Laboratory, with the site divided into four main stretches, each of which contained 20-30 tide pools.

Figure S2. Number (Mean + SE) of gastropods present within the quadrat during each minute of the experiment. (See Figure 2 for details; scale of y-axis same as Figure 2).

Figure S3. Number (Mean + SE) of brachyuran crabs present within the quadrat during each minute of the experiment. (See Figure 2 for details; scale of y-axis same as Figure 2).

Figure S4. Number (Mean + SE) of gobies present within the quadrat during each minute of the experiment. (See Figure 2 for details; scale of y-axis same as Figure 2).