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2   make beetles disperse

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4

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ABSTRACT

1. Induced plant responses to herbivory are common and we have learned a lot about the mechanisms of induced resistance and their effects on herbivore performance. We know less about their effects on herbivore behavior and especially on spatial patterns of damage.

2. Theoretical models predict that induced responses can cause patterns of damage to become aggregated, random, or even. A recent model predicted that informed herbivore movement coupled with communication between plants would make damage more even within individual plants. We tested these predictions in the field using a specialist beetle (*Trirhabda pilosa*) that feeds on sagebrush (*Artemisia tridentata*). Both the beetle and the plant are well-documented to respond to damage-induced volatile cues.

3. Beetle larvae were more likely to move from damaged leaves and leaves that had been exposed to volatiles from nearby damaged leaves compared to undamaged control leaves. Previous lab results indicated that beetles were more likely to choose undamaged leaves compared to damaged leaves or those exposed to volatile cues of damage.

4. A comparison of damage patterns early in the season and after completion of beetle feeding revealed that variance in damage among branches decreased as the season progressed; i.e., damage became more evenly distributed among the branches within a plant. Larvae

33 damaged many leaves on a plant but removed relatively little tissue

34 from each leaf.

35 5. Herbivore movement and the spatial patterns of damage that it

36 creates can be important in determining effects on plant fitness and

37 other population processes. Dispersion of damage deserves more

38 consideration in plant-herbivore studies.

39 Key-words: induced resistance, spatial distribution, over-dispersed,

40 herbivore behavior, movement, plant communication, dispersion,

41 *Trirhabda*

42   1 INTRODUCTION

43   Anyone who has collected tree leaves at the end of the growing

44 season knows that finding a leaf with no damage is rare. This pattern

45 is counter-intuitive since many chewing insects (and other animals) are

46 patchily aggregated in nature. This paper will consider one ecological

47 process that could produce the scarcity of completely undamaged

48 leaves.

49   Scientists have been aware of induced plant responses to

50 herbivory for approximately 50 years (Green and Ryan 1972). When

51 plants are damaged by feeding herbivores, they change in many ways

52 and some of these changes make them less preferred and/or less

53 suitable for herbivores. Induced responses propagate over various

54 temporal and spatial scales, although many have been observed to be

55 localized to those tissues that surround the site of damage (Karban and

56 Baldwin 1997). Several of the early ecologists who described induced

57 responses characterized these temporal and spatial changes and their

58 effects on herbivores. For example, experimentally damaged squash

59 leaves produced chemicals that spread from the site of wounding and

60 rapidly changed the attractiveness and palatability of those damaged

61 leaves for beetle larvae (Carroll and Hoffman 1980). Beetles were

62 presumed to have moved away from sites that had been previously

63 attacked since larvae and adults were always found at least 2 m from

64 past feeding scars and beetles were never observed to occupy the

65   same leaf as a conspecific. Edwards and Wratten (1983) examined

66   herbivore damage to leaves of clover and eight forest tree species at

67   the end of the growing season. Although no statistical analyses were

68   performed, they proposed that the pattern of damage was highly

69   dispersed, i.e., all leaves had some relatively low level of feeding

70   damage and few leaves had high levels. These authors speculated

71   that plant responses and subsequent insect behavior could limit the

72   total amount of tissue damage and that damage that was spread

73   evenly among branches within an individual would be less detrimental

74   to the plant than clumped damage.

75   In the decades since researchers first documented induced

76   responses there has been considerable effort to elucidate the

77   mechanisms that were responsible for plant perception and plant

78   reactions to herbivores. Far less emphasis has been placed on

79   understanding the spatial extent of induction and its consequences.

80   Edwards and Wratten (1983) observed that insects tended to move

81   away from damaged leaves and that this pattern of movement could

82   produce an even pattern of damage at the scale of individual plants.

83   Many herbivorous insects have been found to move away from

84   previously damaged tissues (e.g., Edwards and Wratten 1983,

85   Bergelson, Fowler, & Hartley 1986, Harrison and Karban 1986, Roslin et

86   al. 2008, Kallenbach, Bonaventure, Gilardoni, Wissgott, & Baldwin

87   2012, Perkins et al. 2013, Morrell and Kessler 2017). Although this

88   pattern is commonly found, exceptions have also been noted even for

89   insect species that feed on the same plants reported in the studies

90   above (e.g., Carroll and Hoffman 1980, Bergelson and Lawton 1988).

91   Herbivores that avoid plant tissues that have been damaged

92   previously are considered to exhibit 'informed herbivore movement'

93   (sensu Rubin, Ellner, Kessler, & Morrell 2015). There has been little

94   consensus concerning whether informed herbivore movement will

95   produce even damage to host plants. For example, models of

96   herbivore movement away from damaged-induced plant tissue often

97   predict that herbivores will aggregate at tissues of higher quality

98   (Underwood, Anderson, & Inouye 2005, Anderson, Inouye, &

99   Underwood 2015). This was the pattern observed for beetles on

100   damaged soybean foliage (Underwood, Anderson, & Inouye 2005). A

101   more complex model that included informed herbivore movement as

102   well as volatile communication between neighboring plants was

103   parameterized with empirical data from *Trirhabda virgata* beetles

104   feeding on goldenrod; this model generated distributions that ranged

105   from even to aggregated (Rubin, Ellner, Kessler, & Morrell 2015).

106   These authors found that induced plant resistance tended to lead to

107   patterns of aggregated damage but the addition of both informed

108   herbivore movement and communication between plants spread the

109   damage more evenly.

110   Although there is considerable empirical evidence that many

111   herbivores preferentially move away from damage (informed

112   movement), the effects of this movement on the distribution of

113   damage is poorly understood. It is not known how movement affects

114   the distribution of damage for plant species that respond to cues

115   emitted by damaged neighbors although many plants have been found

116   to exhibit these responses (Karban, Yang, & Edwards 2014).

117   Sagebrush (*Artemisia tridentata*) induces resistance when directly

118   attacked by herbivores or when exposed to damage-associated VOCs

119   produced by experimentally wounded tissue of neighbors (Karban,

120   Shiojiri, Huntzinger, & McCall 2006). In this case, induced resistance

121   was assayed by measuring reductions in the total herbivore damage

122   accumulated over the growing season. Behavioral assays have also

123   been conducted in petri dishes in the lab involving locally abundant

124   chrysomelid beetle larvae (*Trirhabda pilosa*) presented with induced or

125   uninduced sagebrush leaves (Grof-Tisza, Karban, Pan, & Blande 2020).

126   These bioassays indicated that beetles consistently chose undamaged

127   control leaves in preference to leaves that had been either damaged or

128   exposed to volatiles from damaged leaves. In this current study we

129   asked whether beetle larvae in the field were more likely to move to

130   another leaf if the leaf they were on was experimentally clipped or

131   exposed to volatiles from a nearby damaged leaf compared to

132   controls. We then asked whether this movement reduced the variation

133   in damage among branches within sagebrush plants. We flagged all of

134   the branches on study plants and recorded whether the distribution of

135   damage changed from the beginning to the end of the time when

136   these univoltine beetles fed on sagebrush.

137   2 Methods

138   *2.1 Study System*

139   Sagebrush is the most abundant and the defining plant of the

140   Great Basin biome of western North America (Young, Evans, & Major

141   1988). This study was conducted at the UC Valentine Eastern Sierra

142   Reserve (N 37.631 W -118.996) at an elevation of 2550 m, near

143   Mammoth Lakes, CA. Several subspecies of sagebrush co-occur at this

144   study site although only the subspecies *vaseyana* was considered in

145   this study. As a result of its abundance and widespread distribution,

146   sagebrush serves as the host for a large list of insect and vertebrate

147   herbivores (Wiens et al. 1991, Sanford and Huntley 2010).

148   Bushes at the study site were attacked by a specialist

149   chrysomelid beetle (*Trirhabda pilosa*) during the summers of 2017 –

150   2019. This outbreak may have occurred in previous summers but

151   escaped our notice. Populations of this beetle are very patchy such

152   that some bushes had 100% of their leaves attacked while those less

153   than 1 km away supported no larvae. Eggs overwinter in the soil or

154   under bark and larvae begin feeding on foliage at the elevation of this

155   study in late June or early July (Pringle 1960). Feeding by larvae of *T.*

156 *pilosa* is recognizable as rasping damage that leaves a hole or

157 skeletonized pattern with uneven margins in the interior of leaves.

158 This unusual characteristic of damage can be readily differentiated

159 from that caused by the other herbivores of sagebrush in eastern

160 California. Larvae have not been observed feeding on any other host

161 species (Pringle 1960, Karban pers. obs.) Beetles pupate in the soil

162 beneath bushes by mid July. Adults feed on inflorescences and foliage

163 of sagebrush and mate in late July and August.

164   *Movement*

165   We tested whether larvae were more likely to move if the leaf on

166 which they were located was experimentally clipped. We recorded

167 whether 100 individual beetle larvae remained for one hour on the

168 leaves where they were first observed. The leaf or nearby stem was

169 marked with a small piece of colored lab tape. For half of the beetle

170 larvae, the leaf that they were observed on was experimentally clipped

171 with dissecting scissors at the start of the hour-long observation period

172 in the field. Sagebrush leaves have three lobes and one of these lobes

173 was clipped during the treatment. Two other nearby leaves (within 2

174 cm) also had one of their lobes clipped for plants assigned to this

175 treatment. The other beetles served as controls and the leaf they were

176 on plus two others nearby were touched, but not clipped, by the

177 scissors. After one hour, we observed the location of each larva –

178 whether it stayed on the original leaf or moved.

179   Second, we returned to each marked location after 24 hours and

180   recorded whether we could locate each of the beetle larvae on the

181   original branch. We selected plants that had low densities of beetles

182   for this experiment. It is possible that some of the beetles that we

183   located after 24 hours were not the original ones that we had marked

184   the previous day. Because there were few beetles (2-10) on these

185   bushes, this is unlikely and there is no reason to imagine that

186   treatment should have affected the frequency of this outcome. We

187   assume that beetle larvae rarely moved between bushes because we

188   observed similar numbers of beetles on successive days (pers. obs).

189   Third, we tested whether beetle larvae were more likely to move

190   if neighboring leaves were clipped. We marked the location of 100

191   larvae with lab tape. For half of the larvae, we clipped the tip of three

192   leaves that were physically close to each larva (within 2 cm) but not

193   the leaf that the larva was on. Some of the clipped leaves were not on

194   the same stem or sharing vascular connections with the leaf that the

195   larva was on. After 24 hours we recorded whether each larva had

196   moved from its original location.

197   Fourth, we attempted to repeat the experiments by introducing

198   the beetles to leaves receiving different treatments. We tested

199   whether 60 larvae would be more likely to move after 24 hours if they

200   were placed on experimentally clipped leaves compared to being

201   placed on unclipped control leaves in the field.

202   For each of the movement experiments above, we used Fisher's

203 exact test to compare whether larvae were more likely to move from

204 treated leaves compared to untreated controls. Since we had the *a*

205 *priori* expectation that beetles would be more likely to move from

206 damaged leaves or leaves receiving cues from damaged leaves, these

207 tests were one-tailed.

208   *Dispersion of damage*

209   We evaluated the pattern of dispersion of beetle damage on

210 bushes early in the feeding season (July 10) and later after larval

211 feeding had finished (August 24). We mapped all of the branches

212 (mean = 11.7 branches) on 10 bushes and recorded the number of

213 leaves with damage caused by *T. pilosa* and the total number of leaves

214 on each branch both early (July) and late (August). For each branch we

215 calculated the mean number of leaves with beetle damage; a branch

216 was the sampling unit. Since branches had different total numbers of

217 leaves, we standardized these measures by calculating the proportion

218 of damaged leaves per branch. We assessed whether the mean

219 proportion of damaged leaves increased later in the season using a

220 Wilcoxon signed-ranks test with repeated measures of damage (Sokal

221 and Rohlf 1969). Since we had a clear *a priori* expectation, we used a

222 one-tailed test. We chose this nonparametric approach because our

223 damage data could not meet assumptions required for parametric

224 analyses even with transformation (see Supporting Information).

225   We calculated the among-branch variance in proportional

226   damage for each bush to assess if damage variability decreased

227   between July and August. We tested the hypothesis that the variation

228   among branches decreased as the season progressed using a Wilcoxon

229   signed-ranks test with repeated measures of damage (Sokal and Rohlf

230   1969). Since we had a clear *a priori* expectation, we used a one-tailed

231   test. We chose a nonparametric approach because our variance data

232   could not meet assumptions required for parametric analyses, even

233   with transformation (see Supporting Information).

234   Estimating the proportion of leaves that received chewing

235   damage by *T. pilosa* was relatively quick and most importantly, did not

236   require destructive sampling. However, many ecologists are

237   accustomed to estimating damage by chewing herbivores as the

238   percentage of leaf area that is removed. In order to compare these

239   two methods, we removed one branch from 20 sagebrush plants that

240   had varying levels of beetle damage. These branches were collected

241   from another population of *A. tridentata vaseyana* near Tahoe

242   meadows, Mt. Rose, Washoe County, Nevada (N 39.298 W -118.923).

243   For each branch we estimated the number of leaves that had beetle

244   damage standardized for 100 leaves (percent of leaves with damage)

245   and also recorded the percent of leaf area removed by beetles for all of

246   the leaves on each branch. Percent leaf area removed was estimated

247   by photographing each leaf and using the LeafByte application

248 (Getman-Pickering, Campbell, Aflitto, Ugine, & Davis 2019). We

249 compared levels of damage estimated as % leaves with damage, the

250 measure used here, and as % leaf area removed using JMP 14.2 (Fit y

251 by x).

252   We found that the percentage of leaves that had damage by

253 beetles was a good predictor of the leaf area removed (Fig. 1, R^2 =

254 0.51, n = 20, P < 0.001). Since beetles eat only a small fraction of

255 each leaf, the percentage of leaf area removed was approximately an

256 order of magnitude less than the percentage of leaves that were

257 damaged (the slope of the relationship in Fig. 1 was 0.087 $\pm$ 0.020

258 s.e.).

259

260   3 RESULTS

261   *3.1 Movement*

262   Beetles were more likely to move from those leaves that had

263 been clipped compared to unclipped control leaves within one hour

264 following clipping (Fig. 2, Fisher's exact test P = 0.002). After 24

265 hours, those beetles that had been on clipped leaves were more likely

266 to have departed the branch compared to beetles on unclipped

267 controls (Fig. 3, Fisher's exact test P = 0.02). Beetles that moved

268 under these circumstances were most often not in the vicinity and had

269 traveled some unknown distance. Since it was not feasible to mark the

270 beetles themselves without affecting their behavior, we were unable to

271 determine how far they had moved.

272   The results were similar when nearby leaves were clipped but

273 the leaf that the beetles were first on was not disturbed in either

274 treatment. In this case, beetles were more likely to depart leaves

275 whose neighbors had been experimentally clipped compared to those

276 with unclipped neighboring leaves after one hour (Fig. 4, Fisher's exact

277 test P = 0.02).

278   There was no difference in the likelihood that beetles placed on

279 damaged leaves would move compared to beetles placed on

280 undamaged leaves. For both of these treatments, 21 of 30 beetles

281 moved off the leaf they had been placed on within the first hour

282 (Fisher's exact test P = 1.00). Placing the beetles on experimental

283 leaves appeared to agitate them and they moved almost immediately

284 in most cases.

285   *3.2 Dispersion of damage*

286   The ten bushes that we selected to examine patterns of

287 dispersion of damage ranged from having 4 to 65 percent of their

288 leaves with damage during the early sampling event in July (Fig. 5A,

289 mean 25 % of leaves had chewing damage). As the season

290 progressed, more leaves received damage (the mean proportion of

291 damaged leaves increased from 25% to 34%, Wilcoxon signed-ranks

292 test, P = 0.01). Over this time period, the variance in the proportion of

293   leaves with damage decreased by 52% (Fig. 5B, Wilcoxon signed-ranks

294   test, P = 0.019). Variance in the proportion of leaves decreased for 8

295   of 10 bushes even as the mean level of damage increased (Fig. 5C).

296   The pattern of damage became less aggregated (more even) across

297   the branches on individual plants.

298   4 DISCUSSION

299   We have learned a lot about the mechanisms of induced

300   resistance and about their effects on the survival and performance of

301   herbivores. However, we still know relatively little about how they

302   affect the population dynamics of herbivores, particularly their spatial

303   dynamics (Karban 2011, Rubin, Ellner, Kessler, & Morrell 2015). This is

304   somewhat surprising since early reports of induced resistance against

305   herbivory were motivated by observations of striking spatial patterns

306   of damage (e.g., Carroll and Hoffman 1980, Edwards and Wratten

307   1983). Edwards and Wratten argued that herbivores would move away

308   from damaged tissue and that this induced movement would create an

309   even distribution of plant damage. For these early model systems, it is

310   still not known whether either the plants or herbivores use volatile

311   information to induce plant resistance or for informed herbivore

312   movement.

313   Two theoretical models have considered the spatial distributions

314   of damage that are predicted by induced plant responses. Underwood,

315   Anderson, & Inouye (2005) modeled herbivore movement caused by

316 induction and found that herbivores tended to move away from

317 damage and to aggregate at tissues of higher quality. Either

318 aggregated or even distributions could result depending upon the time

319 lags between initial damage, plant responses, and subsequent

320 movement. A more recent model that included both informed

321 herbivore movement and communication between plant tissues that

322 affected induction found that time lags and the magnitude of informed

323 herbivore movement and plant communication all influenced the

324 distribution of damage (Rubin, Ellner, Kessler, & Morrell 2015). These

325 models both predicted that aggregated, random, or even distributions

326 can be expected. Informed herbivore movement led to aggregated

327 damage but the combination of informed movement plus plant

328 communication spread damage more evenly (Rubin, Ellner, Kessler, &

329 Morrell 2015).

330   The current study is the first empirical test of predictions of

331 Rubin et al.'s model in a system in which both herbivores and plants

332 are known to use volatile information emitted by nearby plant tissues.

333 *T. pilosa* larvae in the field were found to move away from leaves that

334 were experimentally damaged (Figs. 2, 3) or were exposed to volatiles

335 from experimentally damaged leaves (Fig. 4). They were more likely to

336 choose to feed on leaves that were neither damaged nor exposed to

337 volatiles from damaged neighbors in lab trials (Grof-Tisza et al. 2020).

338 Sagebrush also perceives cues emitted by damage and becomes more

339   resistant to herbivores when it is exposed to volatiles from

340   experimentally damaged tissue of the same or neighboring individuals

341   (Karban, Shiojiri, Huntzinger, & McCall 2006).

342   As the season progressed, beetle larvae damaged a greater

343   percentage of leaves (Fig 5A). We found that the non-destructive

344   estimates of the proportion of leaves that were damaged by herbivores

345   and destructive measures of leaf area removed were reasonably well

346   correlated (Fig. 1). Not only did the mean level of damage increase

347   over the season (Fig. 5A), but the variance in damage among branches

348   on individual bushes decreased (Fig. 5B, C). The distribution of

349   damage became more even as the season progressed and damage

350   accumulated. This result was robust to our analytical methods;

351   analyzing mean residuals for branches during early and late samples

352   gave similar results as those we presented (see Supporting

353   Information).

354   Many induced plant responses have been found to be localized,

355   strongest for the semi-autonomous tissues near to the site of damage

356   (Tuomi, Fagerstrom, & Niemela 1991, de Kroon, Huber, Stuefer & van

357   Groenendael 2005, Zanne, Sweeney, Sharma & Orians 2006). In

358   keeping with this generalization, induced responses of sagebrush to

359   herbivory remain localized and information does not transfer readily

360   among branches through the plant's vascular system (Cook and

361   Stoddart 1960, Karban, Shiojiri, Huntzinger, & McCall 2006). Localized

362   plant responses increase the spatial variation among leaves and

363   branches, i.e., increase within-plant patchiness in traits that affect

364   herbivores. Many plants have recently been found to perceive and

365   respond to volatile cues emitted by damage to neighboring plant

366   tissues (Karban 2015). The effectiveness of volatile plant-plant

367   communication dissipates over relatively short distances (Heil and

368   Adame-Alvarez 2010, Karban 2015). Plant responses to localized

369   volatile cues also tend to increase the patchiness of defensive and

370   nutritive traits that affect herbivores.

371   Sharing information among plant tissues can have the opposite

372   influence of evening out the variation in plant quality. For plants that

373   perceive volatile cues, any particular plant tissue does not need to be

374   damaged itself prior to responding to elevated risk. In this way,

375   volatile communication has the potential to reduce variation in plant

376   quality among tissues within an individual. Rubin et al. (2015) noted

377   that those empirical studies that found that induced resistance made

378   the distribution of damage more even (Edwards and Wratten 1983,

379   Bergelson, Fowler, & Hartley 1986, Silkstone 1987) all described

380   systems in which the number of leaves greatly outnumbered the

381   number of herbivores. In these cases, the herbivores could move away

382   from previously damaged leaves and seek out undamaged ones. This

383   was also the case for *T. pilosa* and sagebrush in this study with the

384   possible exception of two of the ten bushes that experienced

385   approximately 90% of all leaves with beetle damage by the end of the

386   season. For these bushes, beetle larvae fed on most leaves within an

387   individual plant canopy but they consumed relatively little leaf area on

388   any given leaf (Fig. 1).

389   In conclusion, informed movement by *T. pilosa* larvae away from

390   damaged sagebrush leaves over the course of their development had

391   the effect of evening the distribution of damage among branches

392   within individual bushes. The distribution of damage is not well

393   studied but existing evidence suggests that it can be at least as

394   important as the total amount of damage. Herbivores that dispersed

395   their damage had less adverse effects on plant fitness compared to

396   those with the same amount of more aggregated damage (Marquis

397   1992, Mauricio, Bowers, & Bazzaz 1993, Meyer 1998). Since sagebrush

398   is a long-lived perennial, it was not feasible to assess the effects of

399   different spatial patterns of damage on plant fitness in this system.

400   Patterns of dispersion of damage can also affect key population

401   properties such as dynamics and stability (Hassell and May 1973, Ives

402   1991, Cronin 2003); these patterns deserve more consideration in

403   plant-herbivore studies involving systems that are more amenable to

404   addressing plant performance. Distributions of damage that are even

405   rather than aggregated are counter-intuitive; this system provides an

406   example of induced plant responses to volatile cues coupled with

407   informed herbivore movement that shift the distribution of damage

408   towards increased evenness.

417   Authors' Contributions

418   RK designed the study and collected the data. RK and LHY

419   analyzed the data and wrote the paper.

420   Data are available in Dryad https://doi.org/10.25338/B8162M
421

422   REFERENCES

423   Anderson, K. E., Inouye, B. D. & Underwood, N. (2015) Can inducible

424   resistance in plants cause herbivore aggregations? Spatial

425   patterns in an inducible plant/herbivore model. Ecology, 96,

426   2758-2770.

427   Bergelson, J. M. & Lawton, J. H. (1988) Does foliage damage influence

428   predation on the insect herbivores of birch? Ecology, 69, 434-

429   445.

430   Bergelson, J., Fowler, S. & Hartley, S. (1986) The effects of foliage

431   damage on casebearing moth larvae, *Coleophora serratella*,

432   feeding on birch. Ecological Entomology, 11, 241-250.

433   Carroll, C. R. & Hoffman, C. A. (1980) Chemical feeding deterrent

434   mobilized in response to insect herbivory and counteradaptation

435   by *Epilachna tredecimnotata*. Science, 209, 414-416.

436   Cook, C. W. & Stoddart, L. A. (1960) Physiological responses of big

437   sagebrush to different types of herbage removal. Journal of

438   Range Management, 13, 14-16.

439   Cronin, J. T. (2003) Patch structure, oviposition behavior, and the

440   distribution of parasitism risk. Ecological Monographs, 73, 283-

441   300.

442   de Kroon, H., Huber, H., Stuefer, J. F. & van Groenendael, J. M. (2005) A

443   modular concept of phenotypic plasticity in plants. New

444   Phytologist, 166, 73-82.

445 Edwards, P. J. & Wratten, S.D. (1983) Wound induced defenses in

446 plants and their consequences for patterns of insect grazing.

447 Oecologia, 59, 88-93.

448 Getman-Pickering, Z. L., Campbell, A. T., Aflitto, N., Ugine, T. A., &

449 Davis, J. (2019) LeafByte: A mobile application that measures

450 leaf area and herbivory quickly and accurately. bioRxiv.

451 doi:10.1101/777516.

452 Green, T. R. & Ryan, C. A. (1972) Wound-induced proteinase inhibitor

453 in plant leaves: A possible defense mechanism against insects.

454 Science, 175, 776-777.

455 Grof-Tisza, P., Karban, R., Pan, V., & Blande, J. (2020) Assessing plant

456 communication and induced resistance in sagebrush using the

457 sagebrush specialist *Trirhabda pilosa.* Arthropod-Plant

458 Interactions, doi.org/10.1007/s11829-020-09749-6

459 Harrison, S. & Karban, R. (1986) Behavioral response of spider mites

460 (*Tetranychus urticae*) to induced resistance of cotton plants.

461 Ecological Entomology, 11, 181-188.

462 Hassell, M. P. & May, R. M. (1973) Stability in insect host-parasite

463 models. Journal of Animal Ecology, 42, 693-726.

464 Heil, M. & Adame-Alvarez, R. M. (2010) Short signalling distances make

465 plant communication a soliloquy. Biology Letters, 6, 843-845.

466 Ives, A. R. (1991) Aggregation and coexistence in a carrion fly

467 community. Ecological Mongraphs, 61, 75-94.

468   Kallenbach, M., Bonaventure, G., Gilardoni P. A., Wissgott, A. &

469   Baldwin, I. T. (2012) *Empoasca* leafhoppers attack wild tobacco

470   plants in a jasmonate-dependent manner and identify jasmonate

471   mutants in natural populations. Proc. Natl. Acad. Sci. USA, 109,

472   E1548-1557.

473   Karban, R. (2011) The ecology and evolution of induced resistance

474   against herbivores. Functional Ecology, 25, 339-347.

475   Karban, R. (2015) Plant Sensing and Communication. Chicago:

476   University of Chicago Press.

477   Karban, R. & Baldwin, I. T. (1997) Induced Responses to Herbivory.

478   Chicago: University of Chicago Press.

479   Karban, R., Shiojiri, K., Huntzinger, M., & McCall, A. C. (2006) Damage-

480   induced resistance in sagebrush: Volatiles are key to intra- and

481   interplant communication. Ecology, 87, 922-930.

482   Karban, R., Yang, L. H., & Edwards, K. F. (2014) Volatile communication

483   between plants that affects herbivory: a meta-analysis. Ecology

484   Letters, 17, 44-52.

485   Marquis, R. J. (1992) A bite is a bite is a bite? Constraints on response

486   to folivory in *Piper arieianum* (Piperaceae). Ecology, 73, 143-152.

487   Mauricio, R., Bowers, M. D., & Bazzaz, F. A. (1993) Pattern of leaf

488   damage affects fitness of the annual plant *Raphanus sativus*

489   (Brassicaceae). Ecology, 74, 2066-2071.

490   Meyer, G. A. (1998) Pattern of defoliation and its effect on

491   photosynthesis and growth of goldenrod. Functional Ecology, 12,

492   270-279.

493   Morrell, K. & Kessler, A. (2017) Plant communication in a widespread

494   goldenrod: keeping herbivores on the move. Functional Ecology,

495   31, 1049-1061.

496   Perkins, L. E., Cribb, B. W., Brewer, P. B., Hanan, M., Grant, M., de

497   Torres, M., & Zalucki, M. P. (2013) Generalist insects behave in a

498   jasmonate-dependent manner on their host plants, leaving

499   induced areas quickly and staying longer on distant parts. Proc.

500   Roy. Soc. B, 280, 1-9.

501   Pringle, W. L. (1960) The effect of a leaf feeding beetle on big

502   sagebrush in British Columbia. Rangeland Ecology and

503   Management / Journal of Range Management, 13, 139-142.

504   Roslin, T., Syrjala, H., Roland, J., Harrison, P. J., Fownes, S., Matter, S. F.

505   (2008) Caterpillars on the run – induced defences create spatial

506   patterns in host plant damage. Ecography, 31, 335-347.

507   Rubin, I. N., Ellner, S. P., Kessler, A., & Morrell, K. A. (2015) Informed

508   herbivore movement and interplant communication in an

509   individual-based model. Journal of Animal Ecology, 84, 1273-

510   1285.

511   Sanford, M. P. & Huntley, N. J. (2010) Seasonal patterns of arthropod

512   diversity and abundance on big sagebrush, *Artemisia tridentata*.

513   Western North American Naturalist, 70, 67-70.

514 Silkstone, B. E. (1987) The consequences of leaf damage for

515   subsequent insect grazing on birth (*Betula* spp.). Oecologia, 74,

516   149-152.

517 Sokal, R. R. & Rohlf, F. J. (1969) Biometry. San Francisco: Freeman.

518 Tuomi, J., Fagerstrom, T., & Niemela, P. (1991) Carbon allocation,

519   phenotypic plasticity, and induced defenses. In D. W. Tallamy

520   and M. J. Raupp (Eds.). *Phytochemical induction by herbivores*

521   (pp. 85-104), New York: Wiley.

522 Underwood, N., Anderson, K., & Inouye, B. D. (2005) Induced vs.

523   constitutive resistance and the spatial distribution of insect

524   herbivores among plants. Ecology, 8, 594-602.

525 Wiens, J. A., Cates, R. G., Rotenberry, J. T., Cobb, N., Van Horne, B., &

526   Redak, R. A. (1991) Arthropod dynamics on sagebrush (*Artemisia*

527   *tridentata*): effects of plant chemistry and avian predation.

528   Ecological Monographs, 61, 299-321.

529 Young, J. A., Evans, R. A., & Major, J. (1988) Sagebrush steppe. Pages

530   763-769 In M. G. Barbour and J. Major (Eds.). *Terrestrial*

531   *Vegetation of California*. Second Edition. Special Publication 9,

532   Sacramento, CA: California Native Plant Society.

533 Zanne, A. E., Sweeney, K., Sharma, M., & Orians, C. M. (2006) Patterns

534   and consequences of differential vascular sectoriality in 18

535   temperate tree and shrub species. Functional Ecology, 20, 200-

536   206.

537

538   Figure Captions

539   Fig 1. The relationship between the percentage of leaves damaged by

540   beetles and the percent area removed for 20 branches. ($R^2 =$

541   0.51, n = 20, P < 0.001).

542   Fig 2. The number of beetle larvae that moved away from leaves that

543   had been experimentally damaged (clip) versus unclipped

544   controls after one hour.

545   Fig 3. The number of beetle larvae that we were able to locate (stayed)

546   on branches that had been experimentally damaged (clip) versus

547   unclipped controls after 24 hours.

548   Fig 4. The number of beetle larvae that moved away from leaves that

549   had been exposed to volatiles from experimentally clipped

550   neighboring leaves versus unclipped controls after one hour.

551   Fig 5. The proportion of leaves on branches that have been damaged

552   by beetle feeding on ten sagebrush bushes soon after beetle

553   larvae began feeding (July - early season) and after beetle larvae

554   had completed feeding (August - late season). A. Mean

555   proportion of damaged leaves $\pm$ 1 s.e. B. Variance in the

556   proportion of damaged leaves $\pm$ 1 s.e. C. Change in the variance

557   in the proportion of damaged leaves for each of the ten bushes

558   over the season. The darker line indicates two bushes with
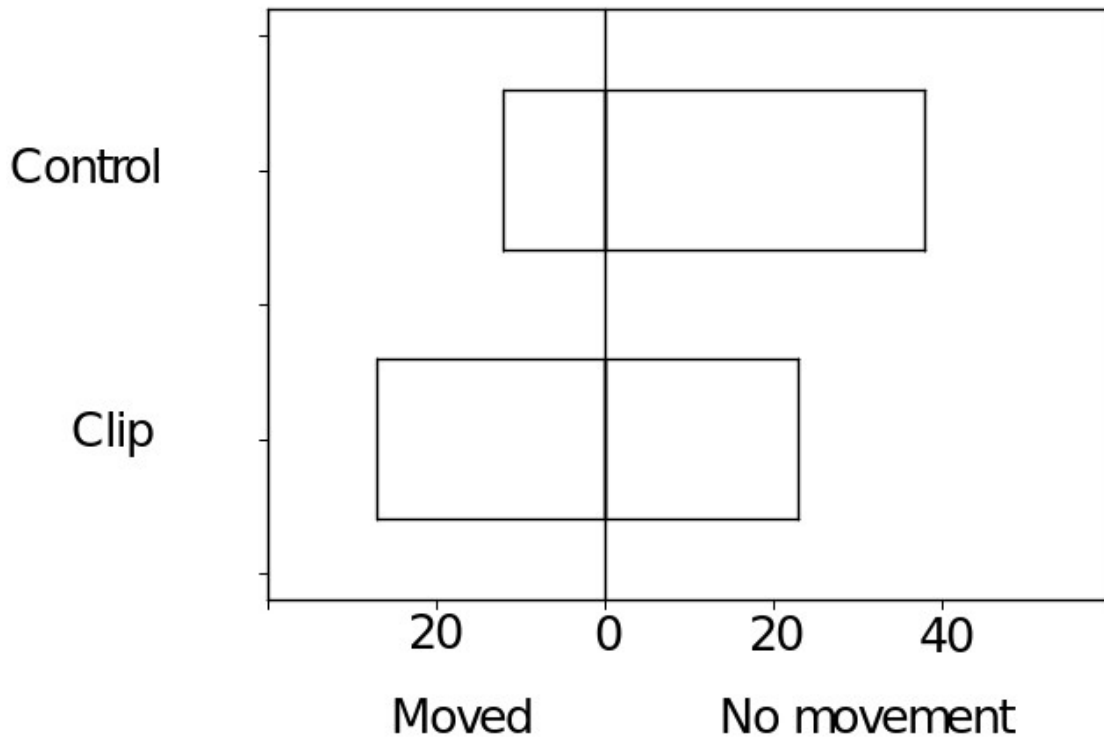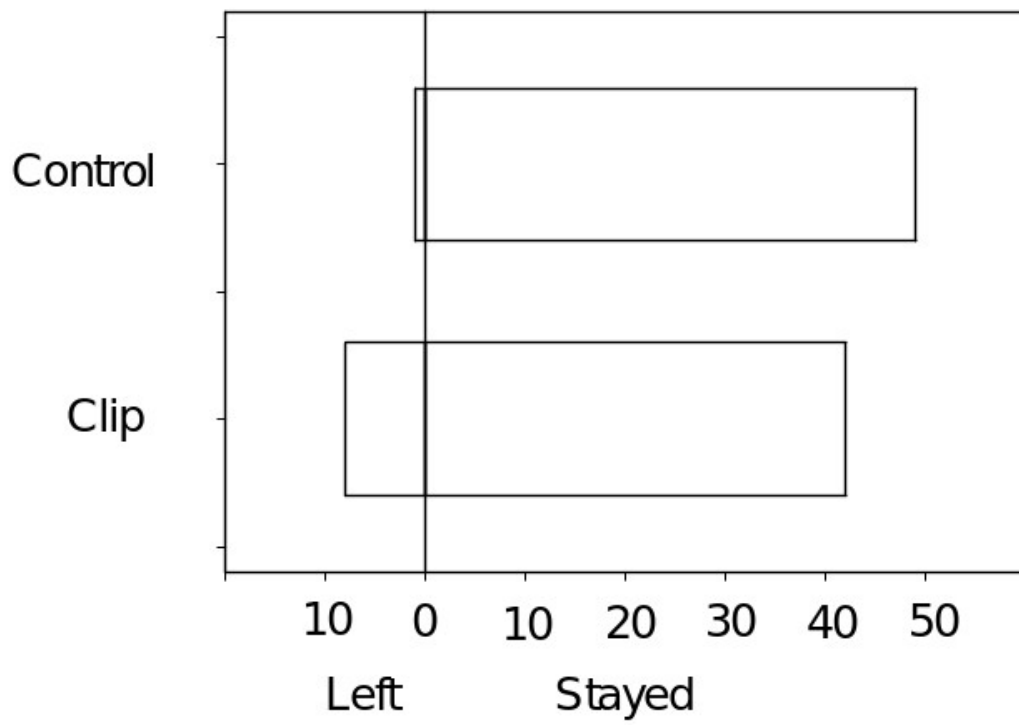
559   similar values.

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562   Fig. 1
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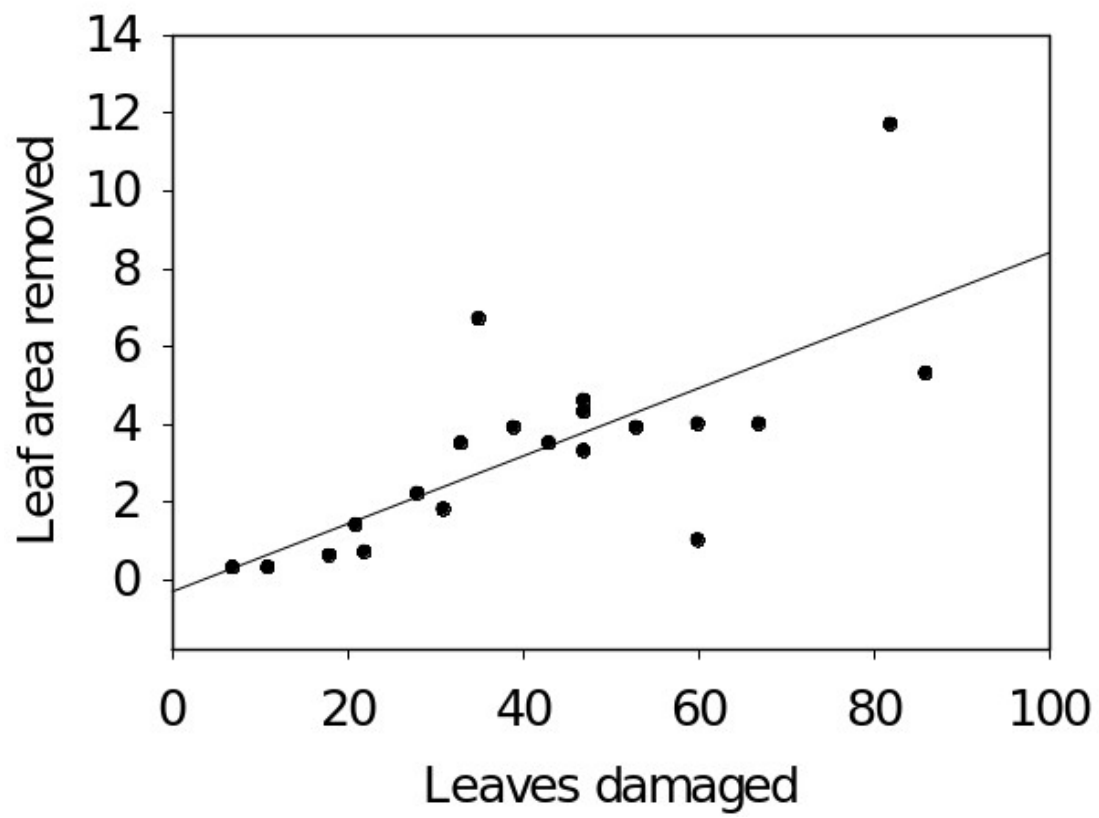
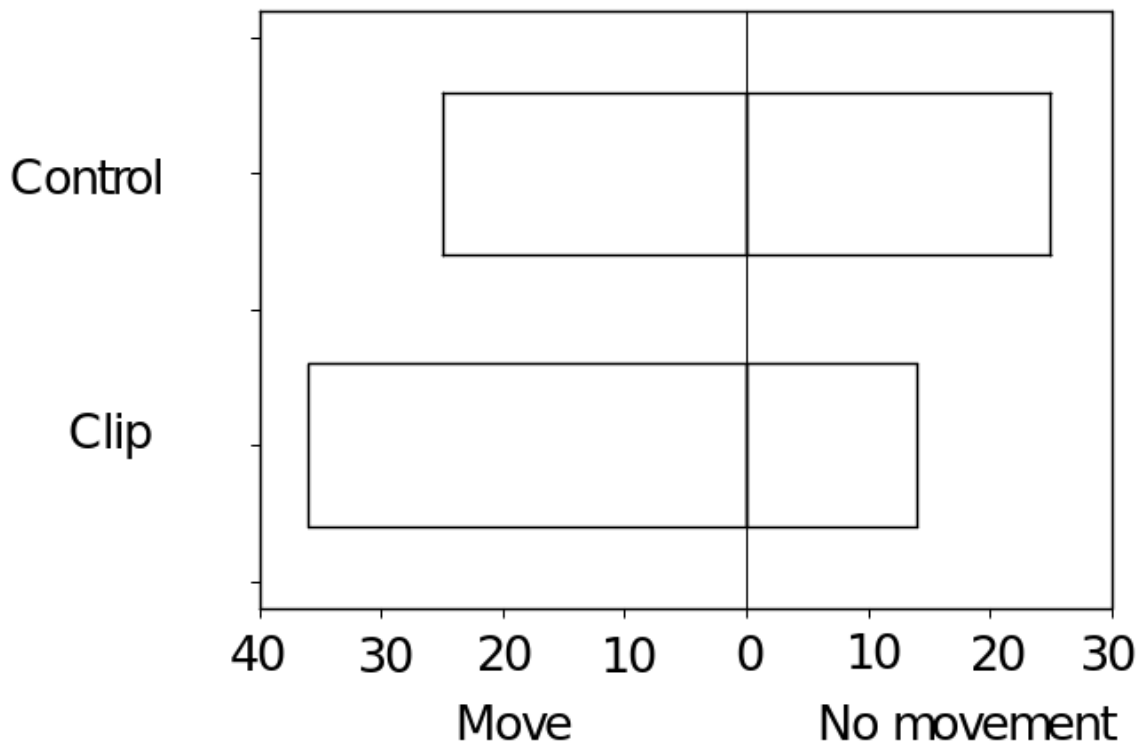564

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566   Fig 2

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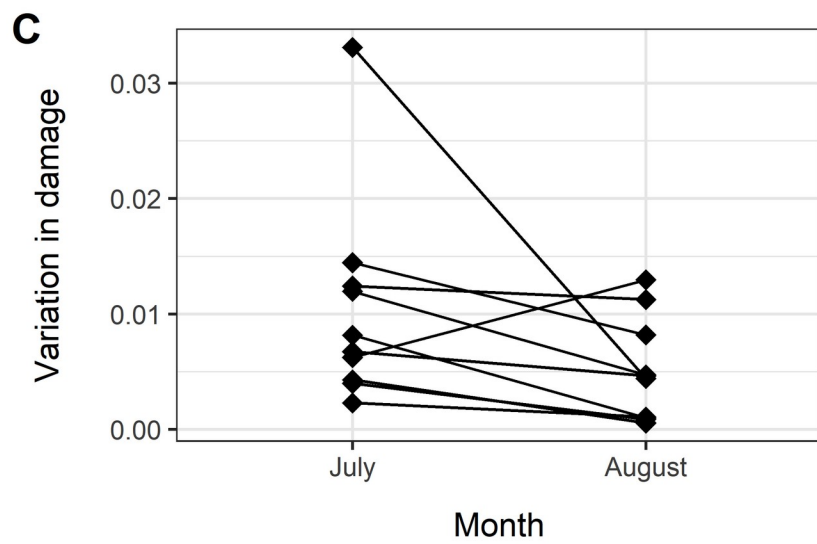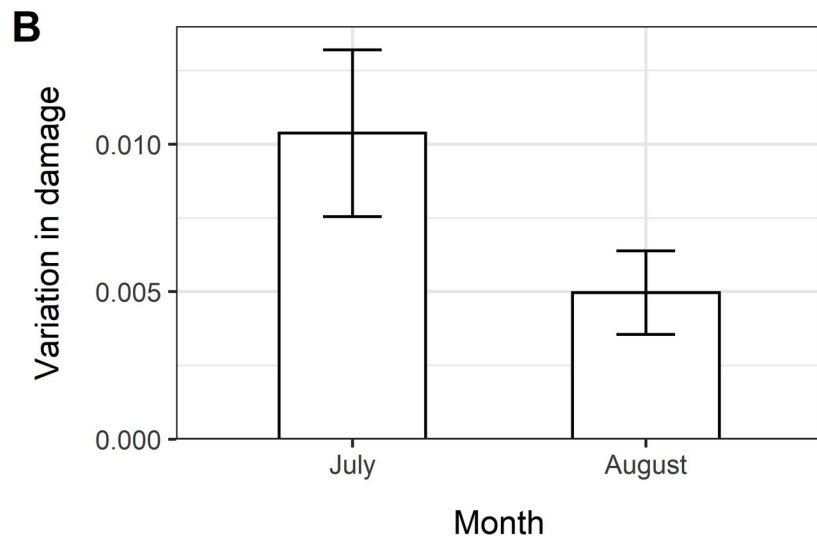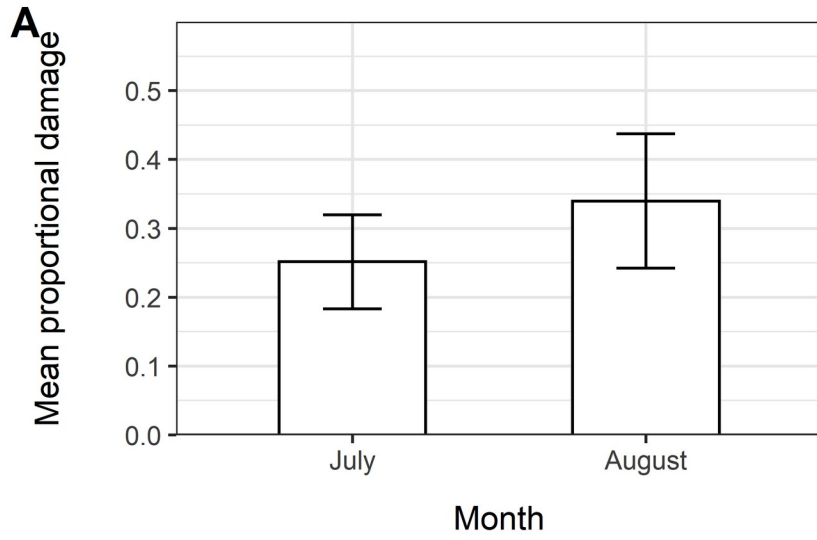
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570   Fig 3
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572   Fig 4

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574   Fig 5

576   Supporting Information

577   *Dispersion of damage*

578   In our paper, we reported that the variation in the proportion of

579   leaves on branches that were damaged by beetles was greater early

580   compared to late in the season (Fig 5B, C). We obtained similar results

581   when we considered the mean absolute residuals (i.e., mean residual

582   deviance) from a linear model with proportional damage as the

583   dependent variable, month as a fixed factor, and bush as a random

584   factor to account for the repeated measures design. While variance is

585   based on the sum of squared deviations, this analysis of residuals uses

586   absolute values and is less sensitive to large deviations. Both analyses

587   yielded qualitatively similar results. Mean absolute residuals decreased

588   by 11.7% between July and August (one-tailed Wilcoxon ranked sum

589   test, P = 0.04). This test is analogous to a non-parametric, repeated

590   measures Levene test for equality of variances.

591   A non-parametric approach was required because the

592   proportional damage data in this study did not meet the assumption of

593   binomial, Poisson or other parametric analyses. While logit

594   transformations are often recommended to allow for the parametric

595   analysis of proportional data (e.g., Warton, D. I., and F. K. Hui. 2011.

596   The arcsine is asinine: the analysis of proportions in ecology. Ecology

597   92:3–10), this dataset included zero values and this made it unreliably

598   sensitive to the size of the arbitrary non-zero constant required to

599   transform these data.