

EFFECTS OF GROUPING BEHAVIOR AND PREDATORS ON THE SPATIAL DISTRIBUTION OF A FOREST FLOOR ARTHROPOD

JASON S. GREAR¹ AND OSWALD J. SCHMITZ

School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut 06511 USA

Abstract. Spatial aggregations arising from social behavior or habitat patchiness are common in nature and have important implications for population dynamics, community stability, and conservation. Distinguishing between these behavioral and environmental causes of pattern is of general interest to spatial ecologists and continues to be a key unresolved issue. Despite the importance of this problem, systematic approaches for resolving the underlying mechanisms are not well developed. We demonstrate here the value of a three-tiered systematic approach involving descriptive spatial sampling, individual-based observation and diffusion modeling, and manipulative field experiments. We used this approach to test social- vs. habitat-driven hypotheses explaining spatial aggregation in the collembolan *Orchesella hexfasciata*. Our results show that aggregation is a gregarious behavior triggered by seasonal increases in soil moisture. Initial field observations suggested that aggregation was habitat driven and associated with soil moisture, but individual-based observations and modeling revealed that moisture was only a triggering mechanism for socially driven aggregation. This was corroborated in field experiments by testing hypotheses that were motivated by the individual-based analyses. Thus, the three-tiered approach led to a more complete understanding of aggregation than would any single technique.

Key words: aggregation; *Collembola*; congregation; diffusion; dispersal; *Gladicosa*; litter; *Lycosidae*; movement; *Orchesella*; patch; predator.

INTRODUCTION

Most animals are locally clustered in their distributions across landscapes. Well-known examples include ungulate herds, bird flocks, fish schools, spawning amphibians, and insect swarms. Attraction toward conspecific individuals is an underlying mechanism in these cases (Pulliam and Caraco 1984, Parrish and Edelstein-Keshet 1999). However, nonsocial behaviors such as attraction to resources also are common and can trigger spatial aggregations that are superficially similar to socially driven patterns.

Theory has shown the stabilizing effects of spatial aggregation on population dynamics (Hassell and May 1974, Mangel and Roitberg 1992). However, predictions from these models depend upon the degree of aggregation (e.g., overdispersion parameters) and are sensitive to the underlying mechanisms driving spatial patterns (Kareiva and Odell 1987, Godfray and Pacala 1992, Ives 1992). Aggregation can arise from individual attraction to habitat features, resource concentrations (Kareiva and Odell 1987, Turchin and Kareiva 1989) or conspecifics (Allee 1931, Okubo 1980, Turchin 1998). Attraction to habitat or resources can be driven by behaviors that maximize nutritional or phys-

iological condition (Belliere and Carrascal 1996), minimize predation risk (Turner and Montgomery 2003), or that represent a trade-off between these requirements (McPeck 1998, Schmitz 1998, Biro et al. 2003, Trussell et al. 2003). Behavioral attraction to conspecifics can arise as an evolutionary response to similar selective pressures but may have unique implications for spatial dynamics. Identifying which mechanisms drive spatial patterns is of general interest to spatial ecologists (Morales and Ellner 2002) and continues to be a key unresolved issue in explaining aggregation (Parrish and Edelstein-Keshet 1999). Our goal here is to help remedy this shortcoming.

To this end, we use a combination of field sampling, modeling, and experiments to explore how different mechanisms contribute to spatial patterning. Many studies have used largely phenomenological approaches such as empirical functions and statistical distributions to describe spatial patterns (Taylor 1961, Lloyd 1967, Usher 1969, Ives 1991). These approaches have revealed the commonness of aggregation in nature and continue to provide important diagnostic tools for empirical studies (White and Bennetts 1996). We began with a similar approach. Nevertheless, statistical descriptions do not reveal mechanisms causing spatial patterns. We gained this mechanistic insight using individual-based observation and diffusion modeling of animal movement (Okubo 1980, Kareiva 1982, Turchin 1998) under experimentally controlled environmental conditions. Taken together, these descriptive and ex-

Manuscript received 30 September 2004; accepted 4 October 2004. Corresponding Editor (ad hoc): J. Bastow.

¹ Present address: Atlantic Ecology Division, Office of Research and Development, U.S. Environmental Protection Agency, Narragansett, Rhode Island 02882 USA. E-mail: grear.jason@epa.gov

perimental approaches provided a powerful set of tools for developing explanations for aggregation that we tested subsequently in a factorial field experiment.

Many classic examples of spatial aggregation are from the Collembola (Elton 1927, Davies 1932, Joosse 1970, Lyford 1975, Verhoef et al. 1977), but causes for aggregation in this group are not well understood. Collembolans (springtails) are good candidates for studying the interplay between social and environmental mechanisms that lead to spatial aggregation because they are abundant in most terrestrial environments, have simple life histories, and live in habitats that are relatively easy to manipulate at the scale of experimental plots. We studied the collembolan *Orchesella hexfasciata* (Entomobryidae) in order to test specific theories and methods for understanding animal aggregation.

BACKGROUND

Natural history

Orchesella hexfasciata dominates the 1–5 mm arthropod community of leaf litter in *Pinus strobus* stands (eastern white pine) at our forest research site in northeastern Connecticut. We observed *O. hexfasciata* feeding on particulate matter visible on decaying *P. strobus* cones (megastrobili) and needles in the lab and found higher densities in *P. strobus* cones lying on the forest floor than in litter.

Moisture is considered the most important environmental factor in the local distribution of temperate forest springtails (Joosse 1981, Verhoef and van Selm 1983, Klironomos and Kendrick 1995, Hopkin 1997). Moisture is strongly correlated with soil temperature (Klironomos and Kendrick 1995) and the activity of microbial food resources (Christensen 1969). Also, moisture may trigger a congregative response in springtails with primitive reproductive biology (Joosse 1970). In such cases, aggregation may affect fertilization success because females must locate spermatophores following deposition in the litter by adult males (Hopkin 1997).

Predation risk may also play a role in springtail aggregation. Collembola are consumed by a wide variety of predators including amphibians (Lima and Moreira 1993), birds (Hopkin 1997), other Collembola (Rusek 1998), chilopods (Poser 1988), spiders (Wise 1993), beetles, lizards, harvestmen, mites, pseudoscorpions, ants, and wasps (see review by Hopkin 1997). On numerous occasions during sorting of litter samples, we directly observed predation on *O. hexfasciata* by spiders (*Gladicosa gulosa* and other lycosids), pseudoscorpions, and mites. We used the lycosid spider *G. gulosa* (forest wolf spider; Brady 1986) in experiments examining predator effects on aggregation. *G. gulosa* is a common litter inhabitant in forests throughout Connecticut (Kaston 1981) that consumes *O. hexfasciata* (J. S. Gear, personal observation).

Hypotheses for springtail aggregation

Spatial distribution in *O. hexfasciata* has not been described, even though aggregation has been reported for other Collembola (Poole 1964, Hale 1966, Joosse and Verhoef 1974, Lyford 1975, Verhoef and Nagelkerke 1977). A few descriptive field studies have considered the behavioral basis for springtail aggregation (Hale 1966, Usher 1969, Joosse 1970), but experimental studies have been limited to laboratory environments (e.g., Joosse and Verhoef 1974, Barra and Christiansen 1975, Mertens and Bourgoignie 1975, Verhoef and Nagelkerke 1977, Bengtsson et al. 2002). Several lab studies have focused on the role of pheromones in springtail aggregation (e.g., Verhoef et al. 1977, Leonard and Bradbury 1984). Taken together, these studies suggest connections between springtail aggregation, moisture variation, reproductive behavior, and conspecific attraction, but they do not consider the effects of environmental patchiness or predators on spatial patterns in the field.

We tested two groups of hypotheses to explain aggregation patterns observed in the field. These hypotheses, which arise from the above discussion of springtail natural history and aggregation, invoke either patch driven or socially (congregation) driven mechanisms.

Patch hypothesis 1: Habitat structure: spatial aggregations are caused by association of animals with habitat patches and therefore do not occur in uniform habitat.—We tested for effects of moisture on individual movement in the lab and on displacement in field release experiments. We also tested for effects of habitat patchiness on aggregation using manipulation of litter moisture patterns and *P. strobus* cone distribution (see *Natural history*) in field enclosures.

Patch hypothesis 2: Predation refuge: spatial aggregations are caused by predator-induced association of animals with specific habitats.—Based on preliminary observations in the field and lab (see *Natural history*), we suspected that *P. strobus* cones might serve as predation refugia. We tested for effects of spiders on springtail use of *P. strobus* cones in the lab and for interaction effects of spider and cone treatments on springtail aggregation in field enclosures.

Congregation hypothesis 1: Conspecific attraction: spatial aggregations are caused by gregarious behavior and can be observed in homogeneous environments.—Previous lab studies of conspecific attraction in the Collembola ruled out effects of environmental patchiness on distribution by using homogeneous lab substrates. Supporting evidence from field studies is lacking. We tested for congregation behavior by observing effects of conspecifics on individual movement in the lab and by testing for the presence of aggregation at differing levels of homogeneity in field enclosures.

Congregation hypothesis 2: Winter congregation: spatial aggregations are caused by a seasonal moisture-induced increase in gregarious behavior.—We

tested for effects of moisture on gregarious behavior using individual-based observations in the lab and by moisture manipulation in the field.

Congregation hypothesis 3: Selfish herding: spatial aggregation is a defensive risk-spreading response to predators.—If grouping behavior is a risk dilution strategy in springtails, aggregation would be expected to persist or increase in the presence of spiders. We evaluated the potential for spiders to affect springtail positioning using lab experiments and tested for spider effects on aggregation by manipulating *G. gulosa* presence in field enclosures.

METHODS

This study was conducted at Yale Myers Forest (YMF) in northeastern Connecticut. YMF is a 3240-ha privately owned research forest. All field work was performed in eastern white pine (*Pinus strobus*) stands, where densities of *O. hexfasciata* estimated from preliminary sampling were highest (0–10 individuals/100 cm³) in comparison to hemlock (*Tsuga canadensis*) and mixed hardwood stands (0–4 individuals/100 cm³).

Estimating aggregation in the field

Evaluations of springtail aggregation often involve goodness of fit tests with the Poisson distribution (Poole 1964, Diggle 1983, Usher and Booth 1986). Departures from the Poisson in the direction of clumping (i.e., spatial aggregation) are typically modeled using the negative binomial distribution (Bliss and Fisher 1953, White and Bennetts 1996, Hilborn and Mangel 1997). We used the Poisson and negative binomial as competing models of springtail distribution in the initial descriptive part of this study.

Preliminary Tullgren funnel extractions (Kempson et al. 1963) and hand sorting of litter indicated considerable variation in density at the scale of decimeters and relatively limited variation below that scale. Therefore, we set up two five-by-five pitfall trap grids in a stand of white pine to assess aggregation at this scale. Traps were spaced 30 cm apart. Each trap consisted of a 25 mm diameter replaceable plastic container inside of a plastic outer sleeve. Neoprene disks were suspended over each trap to reduce rainwater intrusion. Once per month from November 2000 to October 2001, traps were opened, partially filled with ethylene glycol, and removed after two weeks. Traps were not opened in January or February of 2001 due to heavy snow cover. Four hundred trap samples were collected and removed to the lab where *O. hexfasciata* were counted under a dissecting microscope (10 samples were discarded due to flooding). We tested for spatial aggregation using a likelihood ratio test to compare the fit of Poisson and negative binomial models to pitfall array data. We used generalized estimating equations (Liang and Zeger 1986; GENMOD procedure, SAS Institute 2001) for repeated measures analysis to estimate these

likelihoods and to assess the importance of date and plot effects on trap captures.

To evaluate variation in spatial dispersion that occurred in the six months leading up to the observed August peak (see *Results*), we computed likelihoods and Akaike's Information Criteria (AIC) for a series of nested log-linear mixed models:

$$\Pr(Z = y) = \frac{\Gamma(k_{ij} + y)}{\Gamma(k_{ij})y!} \left(\frac{k_{ij}}{k_{ij} + m_{ij}} \right)^{k_{ij}} \left(\frac{m_{ij}}{k_{ij} + m_{ij}} \right)^y$$

$$i = \text{plot} \quad j = t$$

$$m_{ij} = \exp(b_{0i} + b_{1i}t_j + u_{\text{trap}}) \quad (1)$$

where m and k are the mean and dispersion parameters of the negative binomial distribution, t is month, and b_0 and b_1 are intercept and slope parameters. These models used trap-specific random effects (u) to account for the expected correlation between repeated monthly samples from each trap (Booth et al. 2001; NLMIXED procedure, SAS Institute 2001). We compared several models with varying constraints on k : k_{ij} , k_i , k_j , and k_{\dots} .

The dispersion parameter k can only be used as an index of aggregation when m remains invariant between sampled populations (Krebs 1989). Since m varies among our monthly sampling dates, we decided a priori to use the coefficient of variation for the negative binomial as an aggregation index (see *Results* for a post hoc comparison of this CV index to other aggregation indices):

$$\text{CV} = \sqrt{\frac{1}{m} + \frac{1}{k}} \quad (2)$$

Using Monte Carlo simulations and resampled field data, we found that the sampling distribution for this index was well approximated by a gamma distribution. Statistical analyses of CV therefore used the gamma as the underlying distribution.

We examined relationships between monthly pitfall data and soil moisture indirectly using the Brook90 hydrologic model (Federer 1995) to generate daily moisture estimates for the upper 8 cm of the soil profile. Model inputs were daily temperature, precipitation, and wind speed data recorded at a nearby meteorological station in Willimantic, Connecticut for November 2000 to October 2002 (National Weather Service, *available online*).²

Moisture effects on movement and aggregation

Moisture may drive springtail spatial aggregation by creating habitat patchiness or by acting as a cue for gregarious behavior. Before testing these hypotheses in the factorial field experiment, we first examined the effects of moisture on (1) individual passive (i.e., density-independent) movement in the lab; (2) displace-

² (<http://www.erh.noaa.gov/er/box/dailystns.shtml>)

ment following point releases in field mesocosms; and (3) passive and aggregation-limited diffusion in the lab.

Individual-based observation of moisture effects on density-independent movement.—We examined effects of moisture on density-independent movement using release experiments on plaster substrates. Prior to releases, the plaster was either left dry ($n = 18$) or moistened with water ($n = 17$). Our analyses focus on displacement from the release point and total path lengths. Under the assumptions of a simple random walk, the square of displacement distance increases linearly with the number of moves (Okubo 1980, Turchin 1998). We tested for effects of moisture on squared displacement rates after accounting for correlation among repeated measurements along the paths of each individual (MIXED procedure; SAS Institute 2001). To evaluate possible differences in movement activity, we also compared total path lengths for the two treatments using a simple t test with equal variances (F test for equality of variances: $df = 17, 16, P = 0.9811$). See Appendix for additional details.

Release-recapture experiment.—We used circular field enclosures (0.5 m diameter) with homogeneous litter to test for effects of moisture on displacement of *O. hexfasciata* from release points. Eight rectangular sticky traps (3×2 cm) were installed at 10 cm radial distance from the center of each enclosure and flush with the surface of the sifted litter.

We used two moisture levels (control and moistened) and three duration levels (1, 2, and 4 d) in this 2×3 factorial experiment. Five blocks were used in a randomized complete block layout, resulting in 30 experimental units. The duration treatment factor was included to accommodate uncertainty in expected rates of springtail movement in the enclosure settings. We added approximately 84 springtails (see Appendix) to each enclosure at the beginning of the experiment. The response metric was the sum of captures from all eight traps. We used generalized linear modeling with Poisson-distributed errors (GENMOD procedure; SAS Institute 2001) to assess main effects and interactions between moisture and time. The hypothesis being tested was that, if displacement is slower in moist conditions, then fewer springtails would be captured in moist enclosures. See Appendix for additional details.

Modeling effects of moisture on conspecific attraction in the lab.—Pitfall traps in the field revealed seasonal patterns in aggregation that coincide with changes in soil moisture predicted by the hydrologic model (see *Results*). Therefore, we examined potential effects of moisture on conspecific attraction using release experiments on plaster substrates. Techniques were similar to those described in the previous section, except that we used 10-s intervals and a larger arena (0.25 m²) made of plaster drywall. We first recorded density-independent movement in dry and moist conditions in this new setting. To observe movement in the presence of conspecifics, we repeated the above procedure but

recorded the path of one individual in the presence of nine conspecifics. The single and multiple releases were each conducted six times on both dry and moistened plaster, giving a total of 24 recorded paths. Each individual was used only once.

We used the following advection diffusion model to examine ways in which observed movement behaviors could translate into aggregated density distributions (Goel and Richter-Dyn 1974, Turchin 1998):

$$\frac{\partial u}{\partial t} = \beta \frac{\partial}{\partial x}(xu) + D \frac{\partial^2 u}{\partial x^2} \quad (3)$$

where u is density at spatial position x . The first term on the right hand side describes bias up the population gradient proportional to the bias coefficient (β); the last term is the diffusion process proportional to the diffusion coefficient (D). Bias and diffusion in this model can be viewed as counteracting processes. The solution under the conditions used in our study (center point release; zero at $x = \infty$) is a Gaussian distribution for $u(x)$. As t becomes large, the variance of the distribution stabilizes as follows (Turchin 1998):

$$\sigma_z^2 = \frac{D}{\beta}. \quad (4)$$

Taking the square root of both sides (i.e., standard deviation) gives the radius of the area expected to contain 67% of the released population.

Diffusion constants for dry and moist conditions were estimated using the single-release observations of density-independent movement ($D = \text{mean squared displacement}/[4 t]$; Turchin 1998). This gives the same result as setting $\beta \rightarrow 0$ in the solution to Eq. 3. Using these diffusion estimates and the spatial variance from group-release observations of density-dependent movement (σ_t^2), we solved Eq. 4 for β under dry and moist conditions.

Spider effects on behavior

We examined the possibility that springtails move into *P. strobus* cones on the forest floor to avoid predation, causing the high densities of *O. hexfasciata* we observed in these cones. In a simple laboratory experiment, we used the distribution of fecal pellets (frass) within *P. strobus* cones as a proxy for measuring effects of predators on springtail distribution. This followed observation of a clear effect of controlled springtail density (x) on frass counts ($y = 3.318 + 9.237x$, $R^2 = 0.6429$, $df = 11$, $P = 0.0010$; see Appendix).

We used 12 250-mL glass jars with a 1-cm layer of plaster of paris, the distal half of a single *P. strobus* cone, and eight *O. hexfasciata* in each. A single lycosid spider was added to six of these jars and the experiment ran for one week. We summed frass counts from the clearly distinguishable inner tip region of six cone scales from each jar. We also counted frass on a second area, or “inner region,” consisting of the scale midrib

TABLE 1. Summary of predicted and observed treatment effects on aggregation (CV) for hypotheses tested in the field enclosure experiment.

Hypothesis	Treatment	Prediction	Outcome
Patch hypotheses			
Habitat structure	water cone	patchy > uniform	patchy < uniform
Predation refuge	predator × cone	patchy > uniform interaction	NS NS
Congregation hypotheses			
Conspecific attraction	water cone	patchy ≤ uniform	patchy < uniform
Winter congregation	water	patchy ≤ uniform	NS
Selfish herding	predator	control < uniform spider ≥ no spider	control < uniform NS†

Notes: “NS” indicates that there was no significant treatment effect at $\alpha = 0.05$. Details and results of statistical tests are described in *Methods: Field experiment* and *Results: Field experiment*.

† Spiders caused an increase in per capita capture rate, suggesting an increase in movement and an absence of herding.

and a band proximal to the tip region. This allowed separation of springtail positioning responses from spider-induced effects on overall activity by incorporating total frass counts (sum of tip and inner regions) as a covariate in the comparison between spider treatments. We predicted that spiders would cause a shift away from the distal scale tips.

Field experiment

We tested for effects of moisture distribution, lycosid predators, and cone distribution on springtail distribution in forest litter using a three-factor enclosure experiment in a *P. strobus* stand at Yale Myers Forest. We used three moisture treatments (control, patch, and uniform), two predator treatments (stocked and not stocked) and two cone treatments (patch and uniform), resulting in $3 \times 2 \times 2 = 12$ treatment combinations. We applied these treatments in 0.5×0.5 m square enclosures arrayed in a 12×12 latin square design so that each row and column in the array of 144 enclosures contained all 12 treatment combinations. Enclosures were constructed from 20-cm aluminum flashing and installed to a depth of 5–7 cm. The experiment ran from 12 July to 5 September 2002.

Closeable pitfall traps were installed at the center of each of the four quadrants in each of the 0.5×0.5 m square enclosures. We applied water treatments to the enclosures using a backpack sprayer. In the patch treatment, ~50 mL were evenly sprayed into a randomly assigned quadrant (the same quadrants were watered throughout the experiment). In the uniform treatment, each of the four quadrants received ~50 mL. Watering was repeated throughout the experiment two days after either the previous watering visit or the most recent rainfall, so that drying periods for watered areas never exceeded two days. This resulted in 17 watering visits scattered over the 54-d duration of the experiment. Each water application was roughly equivalent to 0.8–1 mm of rainfall over the watered area (<1 L/m²) and was intended only to moisten the surface litter.

Predator treatments were applied by adding a single *G. gulosa* spider to each of the “stocked” enclosures.

We captured these spiders in white pine stands within Yale Myers Forest less than 1 km from the experimental site. During subsequent visits to the field site, we haphazardly observed surviving spiders in 37 (>50%) of the 72 stocked enclosures at least two weeks into the experiment. We used defaunated *P. strobus* cones in the cone treatments. In the patch treatment, four cones were placed in a single quadrant of the enclosure. A single cone was placed in each quadrant for the uniform treatment.

Traps in all enclosures were opened on 5 September and retrieved on 10 September 2002, about eight weeks after treatment applications began. Trap captures were counted under a dissecting microscope. Litter and cones were separately removed from all enclosures in the first three rows of the array to allow estimation of total enclosure abundance using Berlese funnel extraction. These abundances allowed estimation of per capita capture rate.

Spatial aggregation.—By including four traps in each enclosure, we were able to test for effects of treatments on distribution of springtails (Table 1). Based on field data, we used the negative binomial distribution (see *Estimating aggregation in the field*) to model distributions within enclosures ($n = 4$ samples per enclosure). For each enclosure, we estimated m , k , and CV (central tendency, dispersion, and coefficient of variation) by maximizing a likelihood function (Appendix) of the negative binomial (NLP procedure; SAS Institute 2001).

We used CV as the aggregation response variable in statistical analyses. CV is a dimensionless estimate relating dispersion to central tendency and is positively related to clumping. In our experiments, a high CV indicates clumped distribution among the four traps within each enclosure. Based on results of the Monte Carlo simulations described above, we modeled CV error with a gamma distribution in a generalized linear model (GENMOD procedure; SAS Institute 2001, Schabenberger and Pierce 2002). We used this model to evaluate the effects of treatments on CV (i.e., clumpiness) of *O. hexfasciata* spatial distribution.

Total trap counts.—We used the sum of all four traps in each enclosure ($N = 144$) to examine numerical effects of treatment factors on trap counts. As described in greater detail under *Estimating aggregation in the field*, we used a likelihood ratio test to compare fit between the Poisson and negative binomial as underlying distributions for analysis of treatment effects on total trap counts (GENMOD procedure; SAS Institute 2001).

Per capita capture rate.—Effective sampling area is difficult to determine for pitfall trapping techniques (Gist and Crossley 1973) due to the effect of animal activity on per capita capture rate. Trap counts reported here are not intended for direct estimation of absolute densities in the field, but we do make comparisons between treatments. Thus, we assessed treatment effects on per capita capture rate in a subset of the field enclosures.

We used the three rows of enclosures for which we obtained counts of *O. hexfasciata* in the litter and *P. strobus* cones ($N = 36$) to examine water and spider effects on capture rate. We tested for effects of these treatments on total trap counts (sum of traps 1–4), but included total enclosure abundance as a covariate in the model (sum of trap, cone, and litter counts). This allowed assessment of whether treatments caused higher trap captures after controlling for total *O. hexfasciata* density. Covariance-adjusted trap counts were normally distributed, so we used analysis of variance to test for treatment effects (GLM procedure; SAS Institute 2001).

RESULTS

Estimating aggregation in the field

The negative binomial model provided a significantly better fit to the monthly pitfall trap data than did the Poisson (likelihood ratio test, $G = 852$, $df = 1$, $P < 0.0001$), so subsequent analyses were performed with the negative binomial as the assumed underlying distribution. Plot and month of sampling significantly contributed to the model estimated by repeated measures analysis (for plot effect, $\chi^2 = 11.07$, $df = 1$, $P = 0.0009$; for date effect, $\chi^2 = 33.46$, $df = 9$, $P = 0.0001$).

There was an exponential increase in *O. hexfasciata* captures within the period from March to August 2001 (Fig. 1). Based on Akaike information criteria (1201, 1192, 1192, 1190 for k_{ij} , $k_{i.}$, $k_{.j}$, and $k_{..}$, respectively), none of the log-linear models provides a better fit to the data than the one with k reduced (i.e., $k_{..}$, a single dispersion parameter across all months and plots). Since m increases from March to August, the estimated coefficient of variation (CV) decreases, revealing a decreasing degree of spatial clumping in the *O. hexfasciata* count data during this period. This trend is also clearly evident from monthly histograms (Appendix) and from unconstrained estimates of m , k , and CV using

maximum likelihood separately for each month \times plot combination (Fig. 1).

Visual comparison of soil moisture predictions from the Brook90 hydrologic model and monthly CV estimates for springtail distribution (Fig. 1) indicate that the higher and less variable soil moisture levels predicted for winter coincide with periods of highest springtail aggregation.

Moisture effects on movement and aggregation

Individual-based observation of moisture effects on density-independent movement.—The slope of net squared displacement against time was greater for dry than moist conditions ($P < 0.0001$; Appendix). Slope estimates are $0.4 \text{ m}^2/\text{h}$ and $0.2 \text{ m}^2/\text{h}$ for dry and moist conditions, respectively. Total path lengths did not differ significantly between treatments ($df = 33$, $P = 0.5467$). In a post hoc equivalence test (Dixon 1998), a null hypothesis of no effect also could not be rejected (Appendix), so there is insufficient statistical power to draw conclusions about the role of total movement activity on the observed displacement differences. Displacement can also be affected by the directionality of movement, which appears to be slightly lower in moist conditions (Appendix).

Release-recapture experiment.—The number of captures in the field release experiment was significantly affected by both moisture (Fig. 2; likelihood ratio test, χ^2 , $df = 1$, $P = 0.0076$) and duration ($df = 2$, $P < 0.0001$), with moistened enclosures having a lower capture rate (4.6 ± 0.6 [mean ± 1 SE]) than dry controls (6.9 ± 0.7). There were no significant interactions between moisture and duration ($df = 2$, $P = 0.1762$). We interpret these results as evidence that individuals in dry areas disperse more rapidly than those in moist areas. We suspect that the negative effect of duration was due to reduction in trap stickiness caused by a rainfall event that occurred during day 2 of the experiment.

Modeling effects of moisture on conspecific attraction in the lab.—Diffusion coefficients estimated from observations of individual movement in dry and moist laboratory environments are $D = 0.272$ and $0.209 \text{ (m}^2/\text{h)}$, respectively. These results are consistent with other observations of higher displacement under dry conditions. The estimate of β for the moist treatment (0.032) is about twice that of the dry environment (0.014), so there is evidence that attractive bias is stronger in moist environments (Fig. 3). Also, there is slightly greater directionality of movement under dry conditions, as seen in the first release experiment in the smaller arena.

Spider effects on behavior

Spider treatments had a significant effect on the distribution of *O. hexfasciata* frass within *P. strobus* cones in the jar experiments after incorporating total pellet counts as a covariate ($P = 0.0002$). Mean pellet counts on outer regions were 17.8 ± 4.6 (mean ± 1 SD) and

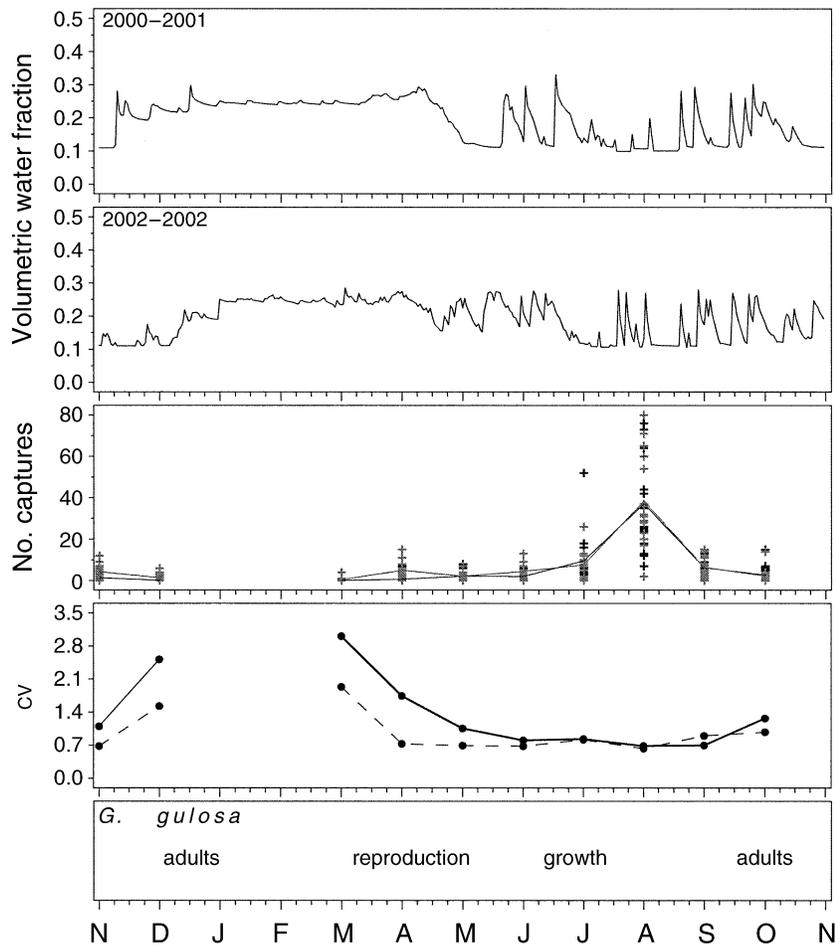


FIG. 1. Soil water volumetric content, *Orchesella hexfasciata* trap captures, and coefficient of variation (CV) for *Orchesella hexfasciata* trap captures, and *Gladicosa gulosa* life cycle. Soil water content is estimated for upper soil horizons (8 cm) using the Brook90 hydrologic model (Federer 1995) with 2000–2002 precipitation data from Willimantic, Connecticut, USA (see footnote 3 for source). Trap captures are total *O. hexfasciata* counts per trap; separate lines are drawn for means from each of two plots ($N = 25$ per plot). CV is estimated from trap data using negative binomial distributions. The *G. gulosa* life cycle is from Brady (1986).

39.8 ± 9.3 for spider and no spider treatments, respectively. Thus, there were fewer fecal pellets on the more exposed tip region of cone scales in the presence of spiders.

Field experiment

Spatial aggregation.—Effects on CV (i.e., aggregation) estimated from fitted negative binomial distributions were significant ($H_0 =$ no effect on fitness of model) only for the water treatment and the column blocking factor (water, $P = 0.0051$; column, $P = 0.0100$; row, $P = 0.1808$; all other effects and second-order interactions $P > 0.45$; Appendix). Estimates of CV were significantly higher for the uniform water treatment than for both patchy ($\chi^2 = 7.53$; $P = 0.0064$) and control treatments ($\chi^2 = 8.12$; $P = 0.0045$). Control and patchy treatments did not differ significantly ($\chi^2 = 0.04$; $P = 0.8320$). The gamma distributions used

to model errors in this test provided a good approximation to observed CV distributions (Fig. 4).

We found similar patterns of aggregation among watering treatments in a post hoc analysis of enclosure data using the standardized Morisita's index of dispersion (I_p) and Green's coefficient (C_g), both of which are considered insensitive to population density (Krebs 1989). Using I_p , the percentage of enclosures in which distributions were significantly clumped (i.e., I_p was above the 95% confidence limit for randomness) were 42, 54, and 60 for control, patchy, and uniform watering treatments, respectively. Green's coefficients for control, patchy, and uniform treatments and their bootstrapped 95% confidence intervals are 0.02 ± 0.01 , 0.05 ± 0.03 , and 0.08 ± 0.04 , respectively.

There was an absence of cone effects on spatial distribution, which contrasted with our expectations from preliminary fieldwork and the observed effects of spi-

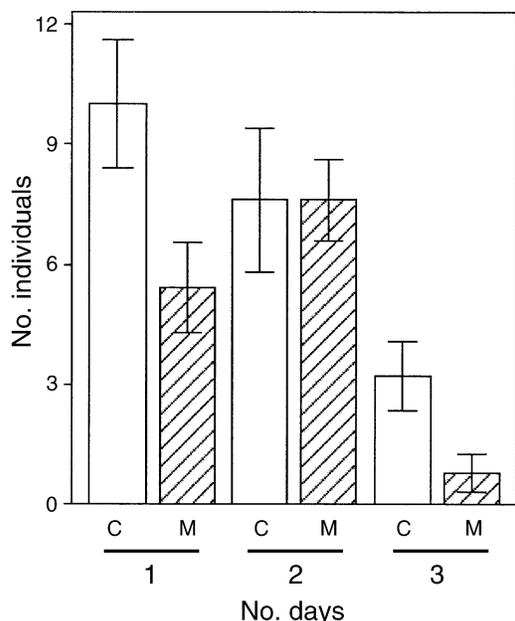


FIG. 2. Results of springtail release experiment, showing effects of control (C; no water added) and moisture (M) treatments on number of individuals (mean \pm 1 SE) caught on traps placed at 10 cm from the release point. Separate enclosures were used for the 1-, 2- and 3-d durations. Each treatment \times duration level was replicated five times.

ders on within-cone distribution in the lab. This may be the result of untested cone effects on stopping probability of moving springtails (orthokinesis). There was a strong positive relationship between trap captures and local cone density around each trap, but our experimental design was neither intended nor suitable for a statistical test of this relationship.

An important factor to consider in trapping studies of aggregation is whether the removal effect of traps on density is sufficiently large to counteract the aggregation response. In particular, this would complicate our interpretation if there were treatment-specific effects on removal. However, such effects appear to have occurred only in the case of spider treatments (see *Per capita capture rate*).

Total trap counts.—The negative binomial provided a significantly better fit to the data than the Poisson ($G = 1759.75$, $df = 1$, $P < 0.0001$), and was therefore used as the underlying distribution in subsequent analyses of total counts (sum of traps in each enclosure). Predator and water treatments (Fig. 5) and the column blocking factor all had significant effects on total *O. hexfasciata* trap captures; there were no significant interactions or cone effects (water, $P = 0.0287$; spiders, $P = 0.0155$; column, $P = 0.0018$; all other effects and second-order interactions, $P > 0.24$; Appendix). Enclosures containing spiders had higher capture rates (89.1 ± 4.8 [mean \pm 1 SE]) than those without (74.1 ± 4.1). In comparison to the water treatment control (83.0 ± 5.3), the patchy treatment was higher ($90.8 \pm$

5.8) and the uniform treatment was lower (71.1 ± 5.7), but only the patchy and uniform treatments differed significantly from each other (Fig. 5).

Per capita capture rate.—The analysis of covariance using the subset of 36 enclosures for which we obtained counts from litter, cones, and traps revealed a significant effect of spiders on distribution among these sources (model, $df = 28$, $P = 0.0143$; spider effect, $df = 1$, $P = 0.0008$). Mean trap counts after covariate adjustment for total enclosure density were 41.7 ± 22.9 (mean \pm 1 SD) in the no spider treatment and 70.9 ± 25.2 in the spider treatment. Spider effects on distribution among habitats are also clearly visible in the raw data (Appendix).

No significant effects were detected for the watering treatment ($P = 0.8132$), spider \times water interactions ($df = 2$, $P = 0.3750$), or row ($df = 2$, $P = 0.0853$). Mean proportions caught in traps (traps/[trap + cone + litter]) were 0.51, 0.55, and 0.52 for the control, patch, and uniform water treatments, respectively, suggesting a nonexistent or negligible effect of water on per capita capture rate.

DISCUSSION

Several striking relationships between population density and environmental patterns in our study system indicate that aggregation is not only the result of density-dependent movement, but that the underlying attraction between individuals changes with seasonally varying environmental conditions. The central challenge in reaching this conclusion was to tease apart active grouping behaviors from the indirect pattern-

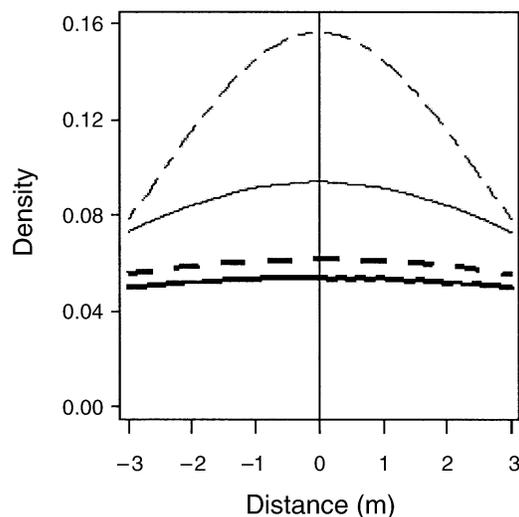


FIG. 3. Comparison of expected densities at increasing distances from the release point (8 h after initial release). Lines correspond to density-independent models in dry ($D = 0.272$ m²/h; $\beta \rightarrow 0$; thick solid line) and moist ($D = 0.209$ m²/h; $\beta \rightarrow 0$; thick dotted line) conditions and density-dependent models in dry ($D = 0.272$ m²/h; $\beta = 0.014$; thin solid line) and moist settings ($D = 0.209$ m²/h; $\beta = 0.032$; thin dotted line).

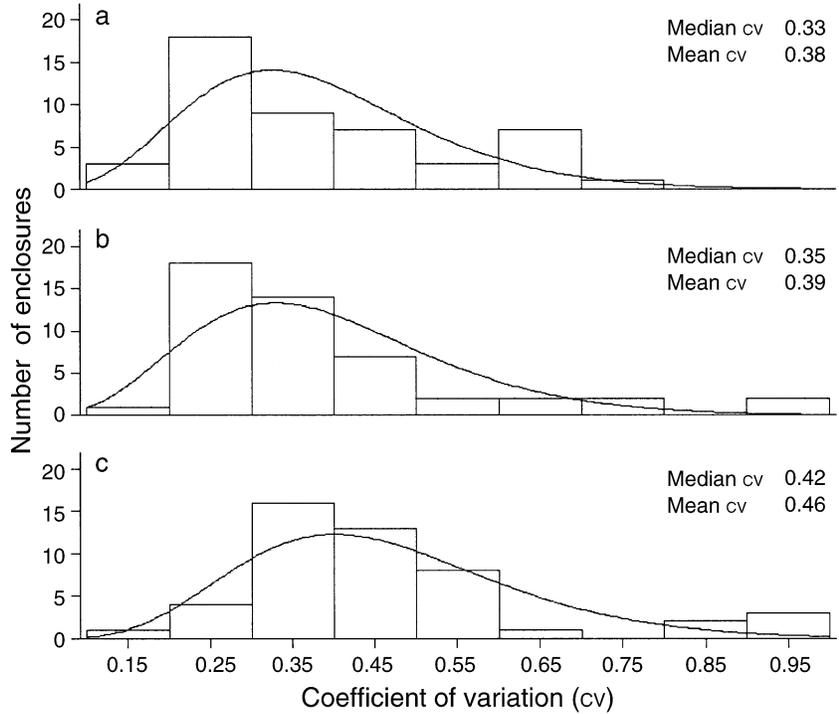


FIG. 4. Histograms and fitted gamma curves for CV estimates from 144 enclosures that received (a) no water application, (b) patchy water application, and (c) uniform water application. CV was calculated from maximum-likelihood estimates of negative binomial distribution parameters using four traps in each enclosure.

forming effects of environmental patchiness. We were able to discern the driving mechanism using a three-tiered approach. First, we quantified the seasonal dynamics of spatial aggregation in the field. Next, we discerned potential explanations for aggregation patterns using individual-based observations and modeling in the lab. Finally, we tested these mechanistic explanations using experiments in natural field conditions (Table 1).

Aggregated spatial patterns in our study were governed more by congregation-driven mechanisms than by environmental patchiness. That is, we observed stronger springtail aggregation within uniformly moist experimental field enclosures than in both the patchy and non-watered enclosures. A similarly positive relationship between overall moisture and aggregation is suggested by the initial study of seasonal distribution patterns, where there was a close match between winter

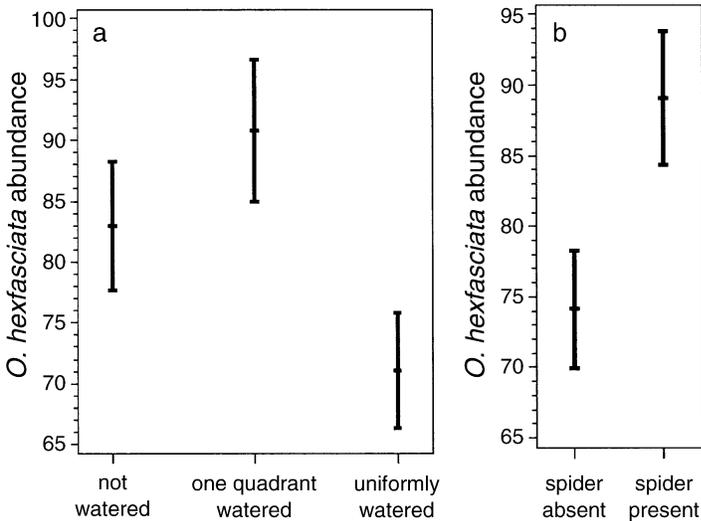


FIG. 5. (a) Effects of water treatments on *O. hexfasciata* abundance (mean \pm 1 SE) as measured by four pitfall traps in each of 144 enclosures ($N = 48$ enclosures per treatment). The contrast between the patchy and uniform treatments is significant ($P = 0.0074$). The control treatment did not differ significantly from the patchy ($P = 0.3101$) or the uniform treatments ($P = 0.0931$). (b) Effects of spider treatments on *O. hexfasciata* abundance (mean \pm 1 SE; $N = 72$ enclosures per treatment; $P = 0.0172$).

aggregation and expected increases in soil moisture (Fig. 1). Thus, it can be inferred from these observations and experiments that aggregation is a seasonal process of moisture-induced attraction between individuals (winter congregation hypothesis).

Although monthly precipitation at the study site is relatively constant throughout the year, seasonal reductions in evapotranspiration cause higher and less variable moisture levels on the forest floor during winter. Seasonal associations between aggregation and winter moisture observed in our study are consistent with winter aggregation patterns in other springtail species (Joosse 1970) that are thought to arise from seasonal reproductive demands.

On the basis of release–recapture experiments and lab observations of density-independent movement reported here, a reasonable argument would have been that aggregation of *O. hexfasciata* is a consequence of attraction to moist habitat patches. However, when we modeled constraints on diffusion due to conspecific attraction, individual attraction affected spatial distributions more strongly than moisture (Fig. 5). This reduced role of habitat patchiness was further elucidated and confirmed by field enclosure experiments, where aggregation remained comparatively strong under uniform moisture conditions.

Predators have been shown to cause indirect positive effects on Collembola (e.g., Rooney et al. 2000), possibly by removing intermediate predators. Our results initially suggested a similar effect since more springtails were caught in enclosures containing spiders. Only after examination of total abundance estimates from litter and cone extraction data did a simpler explanation become clear. Total abundance was lower in these spider enclosures even though trap counts alone were higher. Spiders thus caused an increase in per capita capture rate, which is not surprising given that the springing apparatus of springtails is probably a predation escape mechanism (e.g., Bauer 1985). The positive effect of spiders on trap captures likely resulted from increased movement activity of springtails rather than indirect trophic effects. These results demonstrate that predator-induced behavioral shifts (e.g., Schmitz 1998) can cause sampling biases that should be considered in studies of indirect trophic interactions.

Lycosid spiders have been shown to exhibit type III functional responses (i.e., foraging efficiency increases with prey density) and possibly wasteful killing (reviewed in Wise 1993). In such cases, attack rates increase with prey density with only minor effects of handling time. Since lycosids detect their prey by sensing movement (Foelix 1996), the attack rate would be expected to increase when aggregated prey increase their movement, potentially reducing the benefits of herding as a strategy of risk-aversion in springtails. Thus, grouping behavior is not likely to dilute predation risk over most ranges of prey density (Foster and Trehern 1981, Pulliam and Caraco 1984). These in-

sights and the positive effect of spiders on per capita capture rate in pitfall traps provide evidence against the selfish herding hypothesis as an explanation of spatial distribution patterns in our experimental system.

We found no evidence for or against the predation refuge hypothesis, which would include spider effects on aggregation or interactions with habitat manipulations. Spiders had a strong effect on positioning within *P. strobus* cones, but whether this would lead to larger scale habitat shifts remains unclear.

The moisture-induced changes in spatial distribution observed in this study resulted from the equivalent of roughly 17 mm of added rainfall over an eight week period in late summer (seventeen water applications; 1 mm per application). Average monthly rainfall for this period based on data from 1895–2002 is roughly 100 mm (available online from the National Climatic Data Center),³ so the water treatments represented less than a 10% increase over typical conditions. The sensitivity of our field experiments to this modest water treatment suggests that seasonal shifts in rainfall distribution predicted by global climate change models could have considerable impacts on aggregation-driven components of springtail life history. Weather records for the last 60 years show increases of 2.5 to 7.6 mm per decade during the July to September period while increases for the November to January period range from 7.6 to 15.2 mm per decade (U.S. Temperature and Precipitation Trends, NOAA, *available online*).⁴ This ongoing change represents a shift in rainfall distribution that far exceeds the manipulations to which springtails were so sensitive in our study.

We gave particular attention to conspecific attraction in this study for two reasons. First, changes in local density can depend on the number of conspecifics already present. Second, the clumpy spatial patterns that sometimes result from conspecific attraction can be misinterpreted as indicators of habitat preference or suitability, even when the habitat is uniform from the organism's perspective. Colonial seabirds, for example, are often absent from suitable nesting sites unless an adequate social stimulus is initiated.

Aggregation is a phenomenon that can be explained by a variety of mechanisms. For ecological processes such as species coexistence that are sensitive to these mechanisms, spatial modeling is a valuable and necessary step for revealing the behavioral basis of animal movement. As we show here, this step has become a tractable endeavor. With the ensuing knowledge of cause and effect, forecasting the outcome of ecological interactions relies less heavily on snapshot depictions of clumpy animal distributions.

³ (<http://1wf.ncdc.noaa.gov/oa/climate/research/cag3/CT.html>)

⁴ (<http://www.cpc.ncep.noaa.gov/charts.htm>)

ACKNOWLEDGMENTS

We thank David Skelly, Timothy Gregoire, Michael Booth, Catherine Burns, Heinrich zu Dohna, and Anthony Ives for providing helpful reviews during and after the completion of this work. Erik Crew, Livia DeMarchis, Catherine Burns, Michael Booth, and Elizabeth Kalies helped with the field work. This research was financially supported by a Hutchinson Fellowship from the Yale Institute for Biospheric Studies and grants from Sigma Xi and the Carpenter, Sperry and Mellon foundations to JSG and National Science Foundation grant DEB-0107780 to O. J. Schmitz.

LITERATURE CITED

- Allee, W. C. 1931. Animal aggregations. University of Chicago Press, Chicago, Illinois, USA.
- Barra, J. A., and K. Christiansen. 1975. Experimental study of aggregation during development of *Pseudosinella impediens* (Collembola, Entomobryidae). *Pedobiologia* **15**:343–347.
- Bauer, T. 1985. Beetles which use a setal trap to hunt springtails—the hunting strategy and apparatus of *Leistus* (Coleoptera, Carabidae). *Pedobiologia* **28**:275–287.
- Belliure, J., and L. M. Carrascal. 1996. Covariation of thermal biology and foraging mode in two Mediterranean lacertid lizards. *Ecology* **77**:1163–1173.
- Bengtsson, G., T. Ryden, M. S. Ohrn, and M. Wiktorsson. 2002. Statistical analysis of the influence of conspecifics on the dispersal of a soil Collembola. *Theoretical Population Biology* **61**:97–113.
- Biro, P. A., J. R. Post, and E. A. Parkinson. 2003. Population consequences of a predator-induced habitat shift by trout in a whole-lake experiment. *Ecology* **84**:691–700.
- Bliss, C. I., and R. A. Fisher. 1953. Fitting the negative binomial distribution to biological data and a note on the efficient fitting of the negative binomial. *Biometrics* **9**:176–200.
- Booth, J. G., G. Casella, H. Friedl, and J. P. Hobert. 2001. Negative binomial loglinear mixed models. Unpublished manuscript, Department of Statistics, University of Florida, Gainesville, Florida, USA.
- Brady, A. R. 1986. Nearctic species of the new wolf spider genus *Gladicosa* (Aranae: Lycosidae). *Psyche* **93**:285–319.
- Christensen, M. 1969. Soil microfungi of dry to mesic coniferous-hardwood forests in northern Wisconsin. *Ecology* **50**:9–26.
- Davies, W. M. 1932. Swarming of Collembola in England. *Nature* **130**:94.
- Diggle, P. J. 1983. Statistical analysis of spatial point patterns. Academic Press, London, UK.
- Dixon, P. M. 1998. Assessing effect and no effect with equivalence tests. Pages 275–301 in M. C. Newman and C. L. Strojan, editors. Risk assessment: logic and measurement. Ann Arbor Press, Chelsea, Michigan, USA.
- Elton, C. 1927. Animal ecology. MacMillan, New York, New York, USA.
- Federer, C. A. 1995. BROOK90: a simulation model for evapotranspiration, soil water, and streamflow, Version 3.1. Computer freeware and documentation. USDA Forest Service, Durham New Hampshire, USA.
- Foelix, R. F. 1996. Biology of spiders. Oxford University Press, New York, New York, USA.
- Foster, W. A., and J. E. Trehern. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**:466–467.
- Gist, C. S., and D. A. Crossley. 1973. A method for quantifying pitfall trapping. *Environmental Entomology* **2**:951–952.
- Godfray, H. C. J., and S. W. Pacala. 1992. Aggregation and the population dynamics of parasitoids and predators. *American Naturalist* **140**:30–40.
- Goel, N., and N. Richter-Dyn. 1974. Stochastic models in biology. Academic Press, New York, New York, USA.
- Hale, W. G. 1966. A population study of moorland Collembola. *Pedobiologia* **6**:65–99.
- Hassell, M. P., and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology* **43**:567–594.
- Hilborn, R., and M. Mangel. 1997. The ecological detective. Princeton University Press, Princeton, New Jersey, USA.
- Hopkin, S. R. 1997. Biology of the springtails (Insecta: Collembola). Oxford University Press, Oxford, UK.
- Ives, A. R. 1991. Aggregation and coexistence in a carrion fly community. *Ecological Monographs* **61**:75–94.
- Ives, A. R. 1992. Density-dependent and density-independent parasitoid aggregation in model host-parasitoid systems. *American Naturalist* **140**:912–937.
- Jooisse, E. N. G. 1970. The formation and biological significance of aggregations in the distribution of Collembola. *Netherlands Journal of Zoology* **20**:299–314.
- Jooisse, E. N. G. 1981. Ecological strategies and population regulation of Collembola in heterogenous environments. *Pedobiologia* **21**:346–356.
- Jooisse, E. N. G., and H. A. Verhoef. 1974. On the aggregational habits of surface dwelling Collembola. *Pedobiologia* **14**:245–249.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* **52**:261–282.
- Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *American Naturalist* **130**:233–270.
- Kaston, J. K. 1981. Spiders of Connecticut, revised edition. Bulletin of the State Geological and Natural History Survey of Connecticut **70**:1–1020.
- Kempson, D., M. Lloyd, and R. Ghelardi. 1963. A new extractor for woodland litter. *Pedobiologia* **3**:1–21.
- Klironomos, J. N., and B. Kendrick. 1995. Relationships among microarthropods, fungi, and their environment. *Plant and Soil* **170**:183–197.
- Krebs, C. J. 1989. Ecological methodology. Harper and Row, New York, New York, USA.
- Leonard, M. A., and P. C. Bradbury. 1984. Aggregative behavior in *Folsomia candida* (Collembola, Isotomidae), with respect to previous conditioning. *Pedobiologia* **26**:369–372.
- Liang, K.-Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. *Biometrika* **73**:13–22.
- Lima, A. P., and G. Moreira. 1993. Effects of prey size and foraging mode on the ontogenetic change in feeding niche of *Colostethus stephensi* (Anura, Dendrobatidae). *Oecologia* **95**:93–102.
- Lloyd, M. 1967. Mean crowding. *Journal of Animal Ecology* **36**:1–30.
- Lyford, W. H. 1975. Overland migration of Collembola (*Hypogastrura nivicola* Fitch) colonies. *American Midland Naturalist* **94**:205–209.
- Mangel, M., and B. Roitberg. 1992. Behavioral stabilization of host-parasite population dynamics. *Theoretical Population Biology* **42**:308–320.
- McPeck, M. A. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* **68**:1–23.
- Mertens, J., and R. Bourgoignie. 1975. Some aspects of locomotory activity and gregarious behavior of *Hypogastrura viatica* Tullbe 1872 (Collembola). *Oecologia* **20**:369–376.
- Morales, J. M., and S. P. Ellner. 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* **83**:2240–2247.

- Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, Berlin, Germany.
- Parrish, J. K., and L. Edelstein-Keshet. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* **284**:99–101.
- Poole, T. B. 1964. A study of the distribution of soil Collembola in three small areas in a coniferous woodland. *Pedobiologia* **4**:35–42.
- Poser, T. 1988. Chilopoda as arthropod predators in a beech wood. *Pedobiologia* **31**:261–281.
- Pulliam, H. R., and T. Caraco. 1984. Living in groups: is there an optimal group size? Pages 122–147 in J. R. Krebs and N. B. Davies, editors. *Behavioral ecology: an evolutionary approach*. Sinauer, Sunderland, Massachusetts, USA.
- Rooney, T., C. Antolik, and M. Moran. 2000. The impact of salamander predation on Collembola abundance. *Proceedings of the Entomological Society of Washington* **102**:308–312.
- Rusek, J. 1998. Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity and Conservation* **7**:1207–1219.
- SAS Institute. 2001. The SAS system for Windows. Version 8.2. SAS Institute, Inc., Cary, North Carolina, USA.
- Schabenberger, O., and F. J. Pierce. 2002. *Contemporary statistical models for the plant and soil sciences*. CRC Press, Boca Raton, Florida, USA.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* **151**:327–342.
- Taylor, L. R. 1961. Aggregation, variance and the mean. *Nature* **189**:732–735.
- Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2003. Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. *Ecology* **84**:629–640.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer, Sunderland, Massachusetts, USA.
- Turchin, P., and P. Kareiva. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology* **70**:1008–1016.
- Turner, A. M., and S. L. Montgomery. 2003. Spatial and temporal scales of predator avoidance: experiments with fish and snails. *Ecology* **84**:616–622.
- Usher, M. B. 1969. Some properties of the aggregation of soil arthropods. *Journal of Animal Ecology* **38**:607–622.
- Usher, M. B., and R. G. Booth. 1986. Arthropod communities in a maritime Antarctic moss-turf habitat: multiple scales of pattern in the mites and Collembola. *Journal of Animal Ecology* **55**:155–170.
- Verhoef, H. A., and C. J. Nagelkerke. 1977. Formation and ecological significance of aggregations in Collembola: an experimental study. *Oecologia* **31**:215–226.
- Verhoef, H. A., C. J. Nagelkerke, and E. N. G. Joosse. 1977. Aggregation pheromones in Collembola. *Journal of Insect Physiology* **23**:1009–1013.
- Verhoef, H. A., and A. J. van Selm. 1983. Distribution and population dynamics of Collembola in relation to soil moisture. *Holarctic Ecology* **6**:387–394.
- White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* **77**:2549–2557.
- Wise, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge, UK.

APPENDIX

Additional details of the methods and statistical analyses used in our study and additional results and figures are available in ESA's Electronic Data Archive: *Ecological Archives* E086-051-A1.