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How far away is the next basket of eggs? Spatial memory and perceived cues shape aggregation patterns in a leaf beetle

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Abstract. Gregarious organisms need to handle the trade-off between increasing food competition and the positive effects of group living, and this is particularly important for ovipositing females. We hypothesized that insect females consider how many conspecifics previously visited a host plant. In a no-choice assay, we show that the gregarious blue willow leaf beetle (*Phratora vulgatissima*) laid the most eggs and the largest clutches on plants where a sequence of few individual females was released, compared to plants where one or many different females were repeatedly released. Therefore, this species is more sensitive to the indirectly perceived number of conspecifics than the directly perceived number of eggs on a plant. We further hypothesized that females adjust their own intra-plant egg clutch distribution to that of conspecifics and discovered a new behavioral component, i.e., the modulation of distances between clutches. Females adjusted these distances in ways indicating the use of spatial memory, because the largest distance increases were observed on plants with their own clutches, compared to plants with clutches from conspecifics. However, adjustment of aggregation level and distance between clutches occurred only on a suitable, and not on an unsuitable, *Salix* genotype. We conclude that both behaviors should reduce competition between sibling and non-sibling larvae.

Key words: blue willow leaf beetle, Phratora vulgatissima; *clutch size; cognitive map; Coleoptera; density; distance; egg pooling; kin recognition; learning; relatedness;* Salix.

INTRODUCTION

The distribution of individuals should reflect habitat quality, where quality itself partly depends on the inhabitant density (Fretwell 1969). Ideally, individuals should achieve equal fitness because the costs of intraspecific competition are divided equally among them. Yet, empirical (Doligez et al. 2002) and theoretical (Folmer et al. 2012) studies show that suitable patches are left unoccupied due to conspecific attraction leading to aggregations. How these aggregations are formed and which behavioral components are involved is of great interest in many systems.

Female herbivorous insects should choose the most suitable spot for their progeny (Jaenike 1978, Gripenberg et al. 2010). Larval survival normally decreases with increasing egg number due to exploitative competition (Mitchell 1975) and increased predation risks while searching for alternative feeding sites (Matsumoto 1990). Larvae are believed to aggregate to increase predator protection (Denno and Benrey 1997, Hunter 2000), overcome plant defenses (Clark and Faeth 1997), and improve thermoregulation (Joos et al. 1988). Two behavioral components lead to larval aggregation. The first is the choice of where to place the eggs within the landscape (Heisswolf et al. 2006) or plant (Whitham 1978, Silva and Furlong 2012), and can be modulated by predators/parasitoids (Higashiura 1989), the availability and quality of host plants (Obermaier and Zwölfer 1999), and vegetation structure (Meiners and Obermaier 2004). Information about conspecific egg presence might also influence the oviposition choice, but this phenomenon has not been sufficiently investigated. Some species prefer egg-free hosts (Vasconcellos-Neto and Monteiro 1993), some prefer the presence of conspecific eggs (Navasero and Ramaswamy 1993, Raitanen et al. 2013), and some seem to balance larval feeding competition and parasitism threats (Meiners et al. 2005). The second component is the clutch size decision. How many eggs to oviposit in a clutch can depend on resource size (Godfray 1986), resource quality (Bergstrom et al. 2006), and predation/parasitism (Subinprasert and Svensson 1988, Siemens and Johnson 1992).

Siblings/non-siblings from different clutches often share resources and, therefore, face similar predation and competition as progeny from a single clutch. As with Lack's clutch-size hypothesis (Lack 1947, Godfray et al. 1991), which describes the optimal clutch size that produces the highest progeny survival, one could imagine an optimal distance between clutches as an

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additional behavioral component for determining a suitable aggregation level. Recent studies on kin recognition by spider mites have revealed that the dispersal distance in a population can be driven by relatedness (Bitume et al. 2013), and that the spatial distribution of adults on a plant increases with inbreeding (Le Goff et al. 2009). Predatory mites have also been shown to put greater distances between eggs of more distantly related conspecifics (Faraji et al. 2000). Some insects can recognize eggs from conspecifics (Loeb et al. 2000, Zink 2003), but how this affects distances between clutches is unknown.

Both the direct perception of eggs and indirect cues could inform females about the occupancy of a plant by conspecifics. Sex pheromones, aggregation pheromones, feces, and larval defense secretions (Fernandez and Hilker 2007), as well as induced plant volatiles (Dicke and Baldwin 2010), play important roles in determining host suitability and likely affect aggregation behavior. At the same time, insects are able to learn and memorize, but most studies deal with ants, bees, parasitoid wasps, fruit flies, and grasshoppers (Dukas 2008, Wright and Schiestl 2009). Studies on beetles have focused on conditioning (Held et al. 2001) and how larval experience influences adult behavior (Rausher 1983), but while much is known about the spatial memory of bees, wasps, and ants (Srinivasan 2010, Collett et al. 2013) nothing is known about the spatial memory of beetles.

Here, we studied the gregarious blue willow leaf beetle *Phratora vulgatissima* (Coleoptera: Chrysomelidae), which frequently reaches outbreak densities in natural willow stands and plantations (Björkman et al. 2000, Dalin et al. 2009). When beetles begin to lay eggs, more and more beetles aggregate and the area of infestation increases (C. Björkman, *unpublished data*). Ovipositing females, especially at the edge of the infestation, will switch to other plants at some level of conspecific occupancy to avoid drastic decreases in host-plant quality. This study aimed to determine when females will no longer accept already-occupied hosts and whether indirect perception of conspecifics affects this decision. Hence, we go beyond a simple egg/adult density-dependent response approach and examine whether the number of conspecifics on a host plant provides females with additional indirectly perceived information. The aim was not to identify the cues of importance, just to determine if any cues exist. We hypothesized in a first experiment that females would show lower host acceptance (fewer eggs) if they were the only ones on the plant and their choice was not confirmed by the presence of conspecifics, or if they faced an overwhelming number of conspecifics that were indicative of high exploitative competition.

In a second experiment, we investigated whether females modulate the distance between clutches and if they use spatial memory during this intra-plant clutch distribution. We expected to see increases in distances between clutches, because this would reduce exploitative competition among larvae. We hypothesized that females will establish larger distances among their clutches compared to the already-established old clutches on a plant and will lay their new clutches farther away from these old clutches. If the female is the one that established the old clutches, distances should increase even more, since this female can rely on perceived cues and memory. Because hybrid *Salix* genotypes are morphologically and chemically different (Lehrman et al. 2012), not all are equally suitable for this leaf beetle (Stenberg et al. 2010). Therefore, we tested if there is an interaction between host occupancy/clutch distance modulation and host genotype. We expected that host occupancy would become less important if the genotype is a poor host, and that clutch distances would become greater simply due to larger leaves and/or due to lower plant genotype suitability because each larva then needs more leaf area.

Materials and Methods

Study system and general set up

Phratora vulgatissima [L.] adults and larvae skeletonize willow leaves (*Salix* spp.), and these beetles are the most common specialist herbivore of willow in Europe (Peacock and Herrick 2000). Adults overwinter in reeds or under the bark of trees (Björkman and Eklund 2006), emerge in April, feed for about two weeks, mate, and subsequently lay hundreds of eggs on the undersides of leaves in clutches of 1–50 eggs. Hatching larvae feed gregariously during the first and second instar and then solitarily on different leaves during the third instar (Kendall et al. 1996). This is followed by pupation in the soil. Adults emerge in August, feed quickly, and find hibernation sites. Adults probably excrete pheromones that attract other individuals (Peacock et al. 2001).

We grew *Salix* shoots from 20-cm winter cuttings (suitable host [Sv], *S. viminalis* genotype 78183; unsuitable host [Sd], *S. dasyclados* genotype Gudrun) that were placed in cylindrical transparent plastic cages (70 cm height, 30 cm diameter) with a net on top. Beetles were collected in the Uppsala, Sweden area and reared in cages on Sv or *S. cinerea* (a suitable native host). Individuals used in this study consisted of a mixture of field-collected and next-generation beetles from both rearing cages that were randomly distributed over the experiments/treatments. All experiments were performed in a greenhouse (23°C, relative humidity of 80%, light regime 18 h light : 6 h dark).

Experiment 1: Influence of host occupancy level on host acceptance

Here, we investigated host acceptance modulation, and attempted to manipulate not the conspecific density but the number of indirectly perceived other females. At least three days before the start (to exclude wound responses), plants (~60 cm height) were modified by removing side shoots, dried leaves, and leaves not fully expanded at the top. At the start, one female was released onto each plant. Every morning for nine days, the female was removed for ~5 min (time required for catch/release) from the plant it currently occupied and released again based on one of the following three routines forming the treatments: on the same plant again (same host; Sv $N = 10$ plants; Sd $N = 7$ plants), on the next plant among the plants in that treatment (new hosts; Sv $N = 10$ plants; Sd $N = 5$ plants); or onto either the same or the next plant (mixed hosts; Sv $N = 15$ plants; Sd $N = 3$ plants). The five changes to the next plant for mixed hosts were distributed over time and followed the pattern 10110101 (1 signifies change to next plant; 0 signifies same plant again). With these treatments, we achieved plants where females had laid eggs while the number of conspecifics on these plants increased differently (Appendix A). The mixed hosts treatment is most likely closest to resembling the gregarious laying of some eggs followed by moving to another plant. Using the very unsuitable Sd genotype led to the escape of many beetles. Thus, we only used plants that were visited by the desired total number of beetles within each treatment, and this explains the differences in replication numbers. Herbivory can affect host acceptance (Meiners et al. 2005), but this was similar between treatments (only one beetle at a time).

Experiment 2: Influence of cues and memory on clutch distance modulation

Here, we were interested in the clutch distances and the cognitive capability of beetles. Several days before the experiment, we standardized the plants by removing upper and lower leaves and unwanted leaves within the remaining ~25 cm of the shoot in order to ensure similar distances along the shoot between the remaining 10 leaves. By only using older and very similar leaves, we reduced the possible effects of age, nutritional value, leaf area, and vertical position. First we allowed each female to lay eggs for four days on the same plant (treatment: first release; Sv $N = 27$ plants; Sd $N = 28$ plants) and then measured the distances between clutches (distance type: old–old; Appendix A). In the second part of the experiment, which lasted three days (beetles removed for ~5 h), plants that had received eggs were randomly assigned to one of the two following treatments: experienced (Sv $N = 13$ plants; Sd $N = 6$ plants), where we released the same female again onto the respective plant, or naive (Sv $N = 13$ plants; Sd $N = 14$ plants), where we released new ovipositing females that had not yet laid any eggs on any of the plants. We again measured all distances between these new clutches (new–new) and between the new clutches and the old clutches (old–new). Clutch location on the leaf, egg number, leaf area, and distances between clutches were obtained from photographs using the ImageJ software (Appendix A). By adding clutch–petiole distances and the distance between leaves with clutches (measured with a ruler along the shoot), we obtained all distances between all clutches on the 10 leaves on each plant for both *Salix* species. Naturally, the distances between clutches decreased with increasing number of clutches on a plant (Appendix B: Figs. B1 and B2), and we standardized the distances by dividing each distance by the number of clutches on each plant. Based on the proportion of used and not-used leaves for oviposition, we checked if different distances were only due to females ovipositing on leaves with no eggs. Based on the proportion of clutches closer to the leaf petiole than the previous clutch(es) on that leaf, we investigated whether females facilitate larvae reaching new leaves if the leaf is already occupied.

Statistical analyses

The count data from Experiment 1 were analyzed with generalized linear mixed models (GLMMs) with Poisson distributions. The clutch-distance data from Experiment 2 were impossible to model, so we compared mean distances between clutches using the Kolmogorov-Smirnov (KS) test without adjusting the significance levels. A GLMM with a binomial distribution was used to test if females in the second part of Experiment 2 preferred to oviposit on leaves with eggs and if this proportion is affected by the plant species and/or the treatment. By using the leaves that received eggs in the first part and second part of Experiment 2 and using a similar model, we tested if females preferred to oviposit closer to the leaf petiole compared to the old clutches. All analyses were performed using R (R Core Team 2014). For a description of ImageJ, the models, the R packages, and the reasoning for not adjusting the KS test, see Appendix A.

RESULTS

Experiment 1: Influence of host occupancy level on host acceptance

Plant species and treatment affected the number of eggs laid (Table 1). As expected, between two and five times more eggs were laid on the more suitable Sv than on Sd. In line with our hypotheses, most eggs were laid on Sv in the mixed hosts treatment (Fig. 1a) showing that no and overwhelming number of conspecifics result in low host acceptance. The host-specific clutch sizes followed this general pattern (Table 1, Fig. 1b).

Experiment 2: Influence of cues and memory on clutch distance modulation

If an experienced female was released on Sv (experienced), it established clutches at greater distances from each other than on the previous visit, and these new clutches were even farther away from the old clutches (old–old < new–new < old–new; Fig. 2a). Naive females (naive) did not increase the distances between their clutches compared to the conspecific clutch distances but did lay their clutches farther away from the old clutches (old–old = new–new < old–new), although not as far as experienced females. On Sd, naive females increased new–new compared to old–old distances, and experienced females showed the largest increases in

TABLE 1. Analysis of variance (ANOVA) tables from generalized linear mixed models investigating the oviposition behavior of the blue willow leaf beetle *Phratora vulgatissima*.

Question and explanatory variables	χ^2	df	P
Different number of eggs on plant			
Intercept	1820.24	1	<0.001
PS	60.42	1	<0.001
T	59.90	2	<0.001
PS × T	8.47	2	0.01
Different clutch sizes on plant			
Intercept	580.70	1	<0.001
PS	8.19	1	<0.01
T	6.91	2	0.03
PS × T	7.12	2	0.02
Preferred ovipositing on leaves with eggs			
Intercept	20.46	1	<0.001
PS	*2.00*	*1*	*0.15*
TR	*0.04*	*1*	*0.83*
PS × TR	*2.04*	*1*	*0.15*
Clutch closer to petiole than previous clutch			
Intercept	1.65	1	0.19
PS	*1.25*	*1*	*0.26*
TR	*0.91*	*1*	*0.33*
PS × TR	*0.00*	*1*	*0.94*

Notes: Different number of eggs on plant and clutch sizes on plant were addressed in the first experiment; preferred ovipositing on leaves with eggs and clutch closer to petiole than previous clutch were addressed in the second experiment. Nonsignificant values (italicized) were removed stepwise from the final model starting from the bottom row. Variables included plant species (*Salix viminalis*, *S. dasyclados*; PS); host treatment (same host, new hosts, mixed hosts; T), and release treatment (first release, naive, experienced; TR).

distance. There was great variation in the number of clutches and therefore the number of obtained distances (Appendix A: Table A2) and in the length of these distances (Appendix B: Fig. B1). To separate the effect of generally greater distances on Sd due to greater leaf area (Appendix B: Fig. B2) and/or due to increasing distances on an unsuitable genotype, we further standardized the distances based on the total leaf area (Fig. 2b). Except between the old–new distances of the experienced females, no differences between *Salix* species were found. We also examined the proportions of released females ovipositing on leaves with eggs and the proportion of clutches closer to the petiole than the previous clutch (Table 1). Regardless of plant species or the identity of established clutches, unoccupied leaves were used around twice as frequently (77 times; clutches from all plants) as occupied leaves (29 times; clutches from all plants, including multiple choices), but there was no significant difference in the number of times the females laid eggs closer to the petiole (18 times) compared to the previous clutch on a given leaf (11 times).

DISCUSSION

In Experiment 1, females laid more eggs on plants with intermediate occupancy than plants that had been visited by many females or plants that were only visited by one female. We interpret this behavior as indicating that females take into account trade-offs between the advantages and disadvantages of group living during oviposition. Although a similar behavior has been shown for a root herbivore (Robert et al. 2012) and a leaf beetle (Meiners et al. 2005), we are aware of no previous studies demonstrating such fine-tuned behavior with respect to the fitness-relevant trait of oviposition (Navasero and Ramaswamy 1993, Vasconcellos-Neto and Monteiro 1993, Raitanen et al. 2013). The oviposition rate of these beetles is relatively stable over time, a good predictor of fitness, and determined by plant quality (Lehrman et al. 2012). That this gregarious species shows a lower oviposition rate if a female is alone on the plant could originate from the lack of conspecifics confirming its own decision. This behavior, and the behavior to avoid host plants that are too crowded, might have fitness consequences, because females in such situations would continue to search for better resource patches. We did not intend to directly observe switches to an unoccupied plant. But because host acceptance is plant-quality specific, and despite the

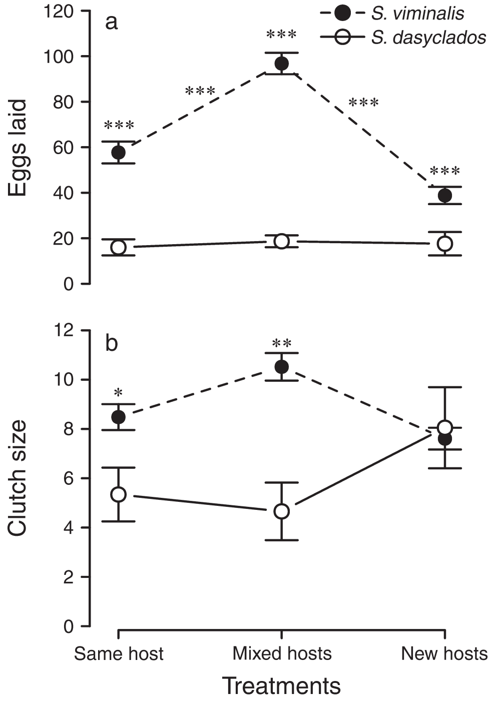

FIG. 1. (a) Number (mean ± SE) of blue willow leaf beetle (*Phratora vulgatissima*) eggs laid and (b) clutch size on a plant after nine days of ovipositing on a suitable (*Salix viminalis*) or an unsuitable (*S. dasyclados*) host plant. Females were released daily onto the same plant (same host), in a rotational manner onto a new plant every day (new hosts), or in an intermediate release pattern (mixed hosts), resulting in the (a) highest host acceptance and (b) largest clutches if females encountered their own and conspecific cues on *S. viminalis*. Significant differences were determined via Tukey contrast.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

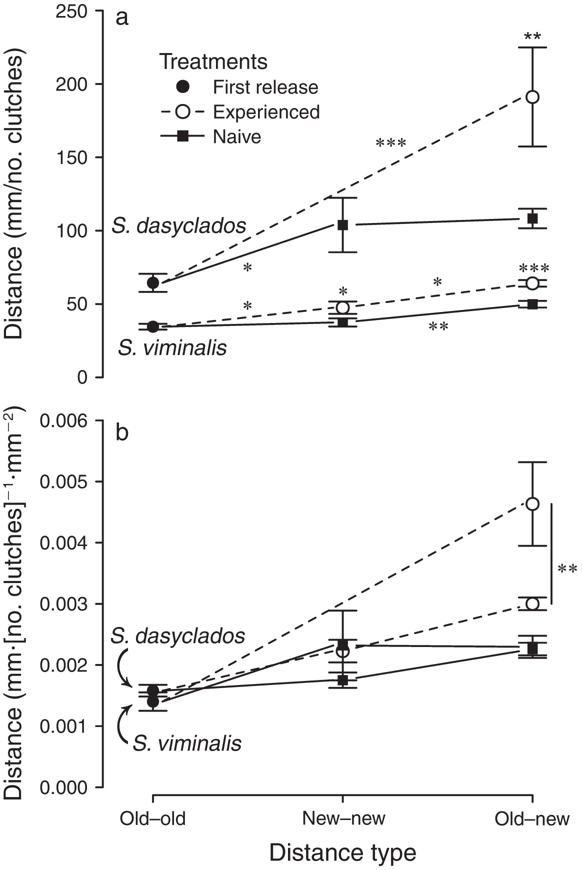

Fig. 2. Distances (mean ± SE) between egg clutches of the leaf beetle (*P. vulgatissima*) on a shoot after (a) correcting for shoots with different clutch numbers and (b) additional correcting for *Salix* species with different total leaf areas; *S. dasyclados* has leaves twice as large as those of *S. viminalis*, and further standardizing of the distances revealed that generally larger distances are due to larger leaves, not to differences in host plant suitability. Largest clutch distances were found among new–new and old–new clutches in part two of the experiment for experienced females that were released on the same respective plants as in part one, and could rely on perceived cues and memory (compare to old–old clutches; old clutches are those laid in part one, new clutches were laid in part two). Naive females released in part two that had not encountered the respective plant before could only rely on cues. Significant differences were determined via a Kolmogorov-Smirnov test.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

fact that females might have left a plant earlier and generally laid fewer eggs out of awareness of alternative host plants, we interpret the observed pattern as finding a suitable level of aggregation that solves the trade-off between increasing offspring food competition and positive effects of group living.

How this species evaluates occupancy is not fully understood. Herbivory combined with beetle presence attracts other adults, suggesting that plant volatiles and pheromones are involved (Peacock et al. 2001), but other cues might also help determine occupancy (Fernandez and Hilker 2007, Dicke and Baldwin 2010). Early eggs probably contributed more to the final number of eggs on a plant than later eggs because females probably laid fewer eggs as they encountered more eggs on a plant over the course of the experiment. This reduced oviposition rate due to increasing egg number occurred in all three treatments and does not explain why the lowest egg numbers were found on plants visited by many females. The assumption that the lower rate is due to the number of conspecifics can, however, explain why the fewest eggs were found in the new hosts treatment (see Appendix B: Fig. B3). Here, the number of conspecifics increased rapidly and females probably responded with a stronger decrease in oviposition rate. The intermediate number of conspecifics resulting in the most eggs indicates that females were more sensitive to how many conspecifics had visited a plant than to the number of eggs on a plant. We also found that the level of aggregation did not differ on the unsuitable host. Here, acceptance was probably so low that striking a balance between competition and group advantages was irrelevant. We also saw that clutch size increased with host suitability. Females might have a physiological constraint and be unable to fully stop producing eggs on unsuitable hosts, resulting in a few small clutches, or because the same leaf area of hosts with different suitability will support different numbers of larvae, females might match clutch size to the nutritional value per leaf area.

In Experiment 2, we were interested in the beetle's cognitive capabilities and used the mean distance between clutches to describe the intra-plant clutch distribution. The largest clutch distances were found for experienced females relying on perceived cues and memory because they themselves established the previous clutches on a plant. This implies that they can memorize some spatial information about their previous oviposition and are able to minimize competition between sibling/non-sibling larvae. The distance modulations between their own clutches and in relation to conspecific clutches are very strong responses and are probably adaptive. They might represent a previously unknown behavioral component of insect oviposition that increases the chances of progeny survival. Such an increase in survival would be due to mechanisms that are relevant to aggregating organisms because the larvae from nearby clutches will form a group. The existence of such fine-tuned distance modulation extends the applicability of the term egg pooling/egg clumping/egg clustering that normally refers to eggs that have contact with at least one other conspecific egg. Arguments for the existence of such modulation should, therefore, be similar to those related to egg pooling and include host-plant nutrient distribution (Chew and Courtney 1991) and increased female fecundity (Courtney 1984). Although females also showed the often-observed behavior of frequently choosing unoccupied leaves (Whitham 1978), this was not the reason for the increased distances, because these choices were independent of plant species and female experience. Previous studies have shown that intra-plant egg distribution varies on host plant species of different suitability (Silva and Furlong 2012), but we showed that leaf morphology in itself might also be important. Females increased the distances between clutches on a less suitable host plant due to differences in leaf area and not host suitability, as we did not find any differences between hosts after standardizing for total leaf area.

Females of the blue willow leaf beetle apparently not only use perceived cues during oviposition and anticipated future larval feeding, but also use some kind of memory to further improve their egg distribution. Learning and memory involve costs (Dukas 2008), but increased fitness due to optimized oviposition should be a strong evolutionary driver and should compensate for these. How these beetles acquire and use their memory in this process, however, remains unexplored. The method of using the final egg distribution as a more indirect proxy than classical movement observations appears to be novel. This method has the advantage of easily showing the existence of spatial memory (or a cognitive map), but the mechanism remains to be identified. Nevertheless, cognitive abilities are assumed to alter trophic interactions and population dynamics (Kondoh 2010), and their effect during oviposition should have major implications, especially for gregarious out-breaking species like *P. vulgatissima*. Both behaviors (finding a suitable level of aggregation and the optimized clutch distances) contribute to the mechanistic understanding of the spread of insect outbreaks.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-1143.1.sm