

Biology 862: Ants & Seed Dispersal
Rebecca Peters - April 25, 2007

- Beattie, A. J. & Lyons, N. Seed dispersal in *Viola* (Violaceae): adaptations and strategies. 1975. American Journal of Botany 62: 714-722.
Thoughtful examination of pros and cons of myrmecochory cf diplochory. Many theories and hypotheses worth consideration, but without stringent experiments to support suppositions.
- Bond, W. & Slingsby, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. 1984. Ecology 65: 1031-1037.
Study showed that Argentine ants are less likely to select myrmecochorous seeds than are native ants; when such seeds are selected, they are not moved a sufficient distance from the parent plant. Authors conclude that some rare, endemic Cape (Africa) plants may be significantly negatively affected.
- Boyd, R. S. 2001. Ecological benefits of myrmecochory for the endangered chaparral shrub *Fremontodendron decumbens* (Sterculiaceae). American Journal of Botany 88: 234-241.
Plant is dispersed by *Messor andrei* (harvester ant). Although various hypothesized benefits of ant dispersal were studied, the only actual benefit appeared to be seedling success post fire because of removal from parent canopy; other hypothesized benefits (general seedling success, seed predation prevention, midden nutrients, etc.) were not found to be significant in this study.
- Bronstein, J. L., Alarcón, R. & Geber, M. 2006. The evolution of plant-insect mutualisms. New Phytologist 172: 412-428.
A comprehensive review of many mutualisms, including myrmecochory. Lists five hypothesized advantages to plants of myrmecochory: avoid seed predators, reduce seedling competition, remove [re: competition/etc.] from adult plant, protect from fire [via burial in ants' nests], and nutrient availability [in nests]. Advantage to ants is assumed to be nutritional; however, this aspect "has received considerably less attention."
- Bülow-Olsen, A. 1984. Diplochory in *Viola*: a possible relation between seed dispersal and soil seed bank. American Midland Naturalist 112: 251-260.
Study focused on evaluating the importance of ballistic primary dispersal because of the high energy requirement for this form of diplochory (ballistic+myrmecochory). Ants were more likely to select seeds that were clumped (negating the importance of ballistic dispersal) and the intensity with which a site was searched for seeds varied greatly. Thus, a possible benefit of diplochory is the establishment of two types of seed banks: one inside and the other outside the nests.
- Christian, C. E. & Stanton, M. L. 2004. Cryptic consequences of a dispersal mutualism: seed burial, elaiosome removal, and seed-bank dynamics. Ecology 85: 1101-1110.**
Studies tested effects of presence/removal of elaiosome and depths of burying on seeds of *Leucospermum truncatum*. Buried seeds escaped most predation but seeds with elaiosomes were at higher risk from fungal attack. Tradeoffs related to various depths of burial were discussed. Additionally, germination was affected by presence/absence of elaiosomes. Authors commented on adverse effects of Argentine ant which does not disperse or bury these relatively large seeds.
- Ciccarelli, D, Andreucci, A. C., Pagni, A. M., & Garbari, F. 2005. Structure and development of the elaiosome in *Myrtus communis* L. (Myrtaceae) seeds. Flora 200: 326-331.
Evaluated elaiosome composition of this species and found only small amounts of lipids, starch, and proteins. Myrmecochory is not ruled out but is thought to be of secondary importance in dispersal of these seeds.

- Culver, D. C. & Beattie, A. J. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *Journal of Ecology* 66: 53-72.
A combination of field and lab work confirmed preferences of several species of ants to various species of *Viola*. Because the distance an ant carried a seed was shorter than the distance the seed was ballistically dispersed, the authors surmise that the primary benefit of ant dispersal is predator avoidance.
- Culver, D. C. & Beattie, A. J. 1980. The fate of *Viola* seeds dispersed by ants. *American Journal of Botany* 67: 710-714.
Study compared the effects of clumping, scarification/elaiosome removal, and relocation to nests. Authors found that only the last (relocation) was statistically significant. However, the first two effects were achieved "mechanically" and additively (seed manipulation) and only the last was observed in the field.
- Dunn, R. R. 2005. Jaws of life. *Natural History* 114: 30-35.
Popular-audience presentation of this ant-plant mutualism. Suggests that ants carry elaiosomes to nest because of corpse-carrying signal. States that this dispersal strategy has evolved "at least eighty-six and perhaps several hundred times around the globe" – in Liliaceae alone, at least eight times. Dunn states that "few cases are known in which a trait has evolved independently as many times as the evolution of elaiosomes."
- Edwards, W., Dunlop, M., & Rodgerson, L. 2006. The evolution of rewards: seed dispersal, seed size and elaiosome size. 2006. *The Journal of Ecology* 94: 687-694.
Showed a strong correlation between seed dispersal and seed size / elaiosome size. Authors were not able to determine which of the latter two factors is the dependent and which is the independent variable.
- Gammans, N., Bullock, J. M. & Schönrogge, K. 2005. Ant benefits in a seed dispersal mutualism. *Oecologia* 146: 43-49.**
Study compared the effects of a controlled ample diet to a ample diet with added elaiosomes. Authors noted a "striking" effect involving production of more and heavier larvae. Elaiosomes of two species of *Ulex* were analysed and both were found to contain 17 free carboxylic acids, in similar abundance. Two essential fatty acids were identified in both species and four sterols were identified from one of the two *Ulex* species.
- Giladi, I. 2006. Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112: 481-492.**
Literature review focusing on three hypotheses for advantages of myrmecochory to plants (dispersal to nutrient-rich site, predator avoidance, distance from parent/siblings). Support was strong for each. Additionally, the author looked at under-researched areas of partner selection and commented on aspects of ant-dispersal which may reflect co-evolution: "myrmecochory, from the plant point of view, is less diffuse than it has frequently been perceived."
- Gómez, C. & Oliveras, J. 2003. Can the Argentine ant (*Linepithema humile* Mayr) replace native ants in myrmecochory? *Acta Oecologica* 24: 47-53.
Study indicates that invasion of Argentine ant is likely to affect ant-related seed dispersal in the Mediterranean area.
- Gómez, C., Espadaler, X., Bas, J. M., & Koerner, C. 2005. Ant behaviour and seed morphology: a missing link of myrmecochory. *Oecologia* 146: 244-246.
Authors looked at how easily seeds can be moved (from nest or midden) after the elaiosome has been removed; concluded that seeds tend to remain in the nest because ants cannot move them without the elaiosome "handle." The exception is large ants which can move relatively smaller seeds outside the typical ant nest distribution "seed shadow."

- Gorb, E. & Gorb, S. 1999. Effects of ant species composition on seed removal in deciduous forest in eastern Europe. *Oikos* 84: 110-118.
Ant species compete for elaiosome-bearing seeds. Also, experienced foragers more quickly identified and dispersed such seeds. Interesting comparison of activities of four ant species in eastern Europe.
- Gorb, E. & Gorb, S. 2000. Effects of seed aggregation on the removal rates of elaiosome-bearing *Chelidonium majus* and *Viola odourata* seeds carried by *Formica polyctena* ants. *Ecological Research* 15: 187-192.
Seed aggregation increased ant dispersal of *Chelidonium majus*; however, this sort of aggregation is unlikely to happen naturally. Conclusion is that the obligate myrmecochor (*Viola*) has a larger seed because of its dependence on ants for dispersal while the ballistically-dispersed seeds of the former plant are smaller and this plant is not as dependent on ants for dispersal.
- Gutián, J. & Garrido, J. L. 2006. Is early flowering in myrmecochorous plants an adaptation for ant dispersal? *Plant Species Biology* 21: 165-171.
Showed that diverse plant species in their study area [in Spain] show "highly synchronous flowering" and fruit production timing. Suggest that this is due to the plant species sharing myrmecochory as a method of secondary seed dispersal. The shared timing is prior to that of non-myrmecochorous plants in the area and also prior to the seasonal appearance of a seed-predacious beetle.
- Gunther, R. W. & Lanza, J. 1989. Variation in attractiveness of *Trillium* diaspores to a seed-dispersing ant. *American Midland Naturalist* 122: 321-328.
Study tested the hypothesis that ants preferentially select seeds with the largest elaiosomes. Results were somewhat supportive and somewhat mixed. A possible cause of this outcome is elaiosome composition which was not studied.
- Handel, S. N. 1976. Dispersal ecology of *Carex pedunculata* (Cyperaceae), a new North American myrmecochore. *American Journal of Botany* 63: 1071-1079.
This species of *Carex* was the first North American member of Cyperaceae to be identified as a myrmecochore. In the study, ants "preferred" seeds of this species over *Carex* seeds without elaiosomes. In simulated nest disturbance, seeds with intact elaiosomes were "rescued" along with larvae.
- Handel, S. N., Fisch, S. B. & Schatz, G. E. 1981. Ants disperse a majority of herbs in a mesic forest community in New York state. *Bulletin of the Torrey Botanical Club* 108: 430-437.
Study involved a field census of plants with known/presumed dispersal methods (myrmecochory, vertebrate-dispersed, abiotic means) and observations of the presence of seed-dispersing ants.
- Handel, S. N., Beattie, A. J. 1990. Seed Dispersal by ants. *Scientific American* 263: 76-83A.
Basically a summary of studies to date. Interesting factoids and leads to other articles.
- Hanzawa, F. M., Beattie, A. J. & Holmes, A. 1985. Dual function of the elaiosome of *Corydalis aurea* (Fumariaceae): attraction of dispersal agents and repulsion of *Peromyscus maniculatus*, a seed predator. *American Journal of Botany* 72: 1707-1711.
Elaiosomes which attract ants were the least-preferred food for deer mice offered a choice of grain, seeds with elaiosomes, and seeds with elaiosomes removed. Authors suggest that the elaiosome of this species repels deer mice, contrary to studies with other plant species in which rodents were attracted to the elaiosome of certain plant seeds.

- Heithaus, E. R., Culver, D. C. & Beattie, A. J. 1980. Models of some ant-plant mutualisms. *The American Naturalist* 116: 347-361.
 Authors present models based on the hypothesis that ant-plant mutualism in re: seed dispersal is stabilized by a third species, a competitor or predator. They conclude that "a stable, feasible equilibrium" is unlikely and that predation is the most likely third factor. The models are based, in part, on theories that have since been shown to be less stable in and of themselves. Would be interesting to know what a "modelist" thinks of this work.
- Heithaus, E. R. 1981. Seed predation by rodents on three ant-dispersed plants. *Ecology* 62: 136-145.
 Using exclusion experiments, the authors showed that secondary ant-dispersal protects primary-dispersed seeds of three eastern US plant species from predation by deer mice.
- Hughes, L. & Westoby, M. 1990. Removal rates of seeds adapted for dispersal by ants. *Ecology* 71: 138-148.
 Removal rates were correlated to temperature, placement, season, and other factors. Seed size affected which ants (by size) could remove the seeds. The authors noted the need for further study on relative benefits granted by different species of ants.
- Hughes, L. & Westoby, M. 1992. Capitula on stick insect eggs and elaiosomes on seeds: convergent adaptations for burial by ants. *Functional Ecology* 6: 642-648.
 Eggs of some stick insect species (Phasmatodea) resemble elaiosome-bearing seeds. Such eggs were carried to ant nests at a rate similar to elaiosome-bearing seeds. These eggs escape wasp predation. Authors cite this as a "striking example of evolutionary convergence between the plant and animal kingdoms."
- Hughes, L., Westoby, M., & Jurado, E. 1995. Convergence of elaiosomes and insect prey: evidence from ant foraging behavior and fatty acid composition. *Functional Ecology* 8: 358-365.
 Fatty acids found in plant elaiosomes were found to more closely resemble composition of insects than of seeds. Authors suggest that adaptive value of elaiosomes "is to shift the odds of a seed being removed by a granivore, towards being removed by a carnivorous or omnivorous ant species."
- Imbert, E. 2006. Dispersal by ants in *Centaurea corymbosa* (Asteraceae): What is the elaiosome for? *Plant Species Biology* 21: 109-117.
 Showed that the presence of an elaiosome does not ensure selection of a seed by ants. Compared benefits (or lack thereof) of various seed burying depth. Results indicated that elaiosome removal decreases germination rate. Raises interesting questions for further study.
- Le Corff, J. 1996. Establishment of chasmogamous and cleistogamous seedlings of an ant-dispersed understory herb, *Calathea micans* (Marantaceae). *American Journal of Botany* 83: 155-161.
 Study showed that ants showed no preference for one seed type over the other (chasmogamous cf. cleistogamous) in regard to dispersal. Seedlings fared differently, perhaps a result of differing light response in various sites.
- López-Vila, J.R.; García-Fayos, P. 2005. Diplochory in *Ulex parviflorus* Pourr. *Acta Oecologica* 28: 157-162.
 Plant ballistically disperses seeds which germinate slowly near parent. Seeds which are secondarily dispersed by ants and which have the elaiosome removed germinate more quickly, probably because elaiosome removal "allows water and air to reach the embryo."

- Lu, K. L. & Mesler, M. R. 1981. Ant dispersal of a neotropical forest floor Gesneriad. *Biotropica* 13: 159-160.
Via observations and exclusion studies, authors determined that ants disperse elaiosome-bearing seeds of *Chrysothenis friedrichsthaliana*.
- Manzaneda, A. J., Fedriani, J. M. & Rey, P. J. 2005. Adaptive advantages of myrmecochory: the predator-avoidance hypothesis tested over a wide geographic range. *Ecography* 28: 583-592.
Tested the hypothesis that myrmecochorous seeds are at reduced risk for predation (by rodents, et al.) once inside the ants' nests. Results were mixed. While some nests were safe sites, others were "risky-microsites" attractive to local rodents. Authors comment that, in general, not enough work has been done on the fate of ant-dispersed seeds post arrival at the nest sites.
- Montesinos, D., García-Fayos, P., & Mateu, I. 2006. Conflicting selective forces underlying seed dispersal in the endangered plant *Silene diclinis*. *International Journal of Plant Sciences* 167: 103-110.
Interestingly, this plant species shows higher seedling survival *near* the parent. High density of seeds increases predation and longer dispersal distance reduces seedling survival.
- Ness, J. H., Bronstein, J. L., Andersen, A. N., & Holland, J. N. 2004. Ant body size predicts dispersal distance of ant-adapted seeds: Implications of small-ant invasions. *Ecology* 85: 1244-1250.
Authors looked at impact of *small* ant invasions on seed dispersal (*Solenopsis invicta*, a red fire ant, and four other small invasive ant species). Found that smaller ants disperse seeds a shorter distance (if at all) and that invasion by small ants will disrupt ant-plant mutualisms, to an extent potentially detrimental to seedling success (because of shorter distance from parent plant and/or lack of burying).
- Oberrath, R. & Bohning-Gaese, K. 2002. Phonological adaptations of ant-dispersed plants to seasonal variation in ant activity. *Ecology*. 83: 1412-1420.
Looked at "24 ant-dispersed and 251 non-ant dispersed plant species." Results indicate the ant-dispersed plant species share an early phenology and thus do not compete w/ non-ant-dispersed plants for ant "resource." The authors' "multiple regression analyses indicate that [the synchronous timing] could be explained only to a small degree by factors such as habitat type, pollination mode, growth form, or seed size." Conclude that plants have adapted to the seasonally active period of ants.
- Ohara, M. & Higashi, S. 1987. Interference by ground beetles with the dispersal by ants of seeds of *Trillium* species (Liliaceae). *Journal of Ecology* 75: 1091-1098.
Study showed that the majority of seeds under observation had the elaiosome eaten by nocturnal ground beetles who did not transport seeds. Seeds with elaiosomes removed by beetles were not secondarily-dispersed by ants, thereby affecting long-range dispersal and resulting in seed clumping near the parent plant. The authors noted that *Trillium* elaiosomes are relatively large compared to those of other ant-dispersed species.
- Ohkawara, K. 2005. Effect of timing of elaiosome removal on seed germination in the ant-dispersed plant, *Erythronium japonicum* (Liliaceae). *Plant Species Biology* 20: 145-148.**
Elaiosome removal, when delayed by one or two days, resulted in higher germination rates in this plant species vs. no removal or immediate removal. The author suggests that the delayed elaiosome removal simulates a signal of ant-dispersal [to nest]. Seed removal by ants and predators was observed in a separate portion of the study.
- Peters, M., Oberrath, R., Böhning-Gaese, K. 2003. Seed dispersal by ants: are seed preferences influenced by foraging strategies or historical constraints? *Flora* 198: 413-420.
Authors looked at seed preference by ants based on (a) plant species within current ant range and (b) plant species found within historic (phylogenetic & ontogenetic) range. Results indicated that seeds are selected predominantly based on size of elaiosomes and that historical constraints do not seem to play a role.

- Retana, J., Picó, X., & Rodrigo, A. 2004. Dual role of harvesting ants as seed predators and dispersers of a non-myrmecorous Mediterranean perennial herb. *Oikos* 105: 377-385.
Harvesting ants are both antagonistic and mutualistic toward seeds. A small, but significant, percentage of seeds harvested by ants (even of non-myrmecochorous plants) benefit – either dropped along path, discarded at nest, etc.
- Rice, B. & Westoby, M. 1986. Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. *Ecology* 67: 1270-1274.
Soil sampling from seedlings germinating at nest sites did not show higher total N or available P than soil around non-myrmecochorous seedlings.
- Rodgerson, L. 1998. Mechanical defense in seeds adapted for ant dispersal. *Ecology* 79: 1669-1677.
Examined mechanical defense of 43 species of seeds (in re: predation risk) by measuring seed strength. Also looked at relationship to 2 seed-removing ant species. Concluded that ants do not select in correlation to seed strength; however weaker seeds are more likely to be consumed or damaged.
- Smith, B. H., deRivera, C. E., Bridgman, C. L., & Woida, J. J., . 1989. Frequency-dependent seed dispersal by ants of two deciduous forest herbs. *Ecology* 70: 1645-1648.
Studies showed that ants selected the "rarer" of two elaiosome-bearing seeds offered, suggesting that plants with synchronous phenology will be able to coexist. Results also indicated that removal to ant nests provides some protection from rodent herbivory.
- Smith, B. H, Forman, P. D. & Boyd, A. E. 1989. Spatial patterns of seed dispersal and predation of two myrmecochorous forest herbs. *Ecology* 70: 1649-1656.
Seeds of two species (from two families) were monitored. Although rodents were present in the study area, predation was not observed. Myrmecochory was affected by edaphic and topographic conditions such that lower ant density resulted in lower numbers of seeds removed; therefore "dispersal is ant-limited when local seed populations are dense."
- Stamp, N. E, Lucas, J. 1990. Spatial patterns and dispersal distances of explosively dispersing plants in Florida sandhill vegetation. *The Journal of Ecology* 78: 589-600.
Ballistic dispersal was not sufficient to escape the adult patch; the added distance of ant-dispersal for seeds with elaiosomes succeeded in moving seeds outside that patch. Larger seeds required larger ants. Not all seeds were transported.
- Vander Wall, S. B. & Longland, W. S. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology and Evolution* 19: 155-161
Review which presents the benefits of various forms of diplochory. Regarding myrmecochory, [it] "is not very effective at colonizing new patches because ants do not carry seeds very far."
- Vander Wall, S. B., Kuhn, K. M., & Beck, M. J. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86: 801-806.**
Brief review noting widespread confusion of "seed dispersal" with "seed predation," particularly during a secondary dispersal stage. Authors note that dispersal may involve three or more steps. Also calls for more research rather than recycling potentially erroneous assumptions that were made in the past.
- Winkler, E. & Heinken, T. 2007. Spread of an ant-dispersed annual herb: an individual-based simulation study on population development of *Melampyrum pratense* L. *Ecological Modelling* 203: 424-438.
Simulations showed that myrmecochory facilitates population spread of studied species but the efficiency of such population effect is site-dependent and thus highly variable.