Ballooning Frequency and Habitat Predictability in Two Wolf Spider Species (Lycosidae: Pardosa)

Matthew H. Greenstone*

Introduction

The first evolutionary ecological treatments of terrestrial arthropod migration appeared in the early 1960's (Johnson 1960; Kennedy 1961; Southwood 1962). Since that time there has been a proliferation of studies on the behavior, physiology, ecology and evolution of migration (see Dingle 1972, 1978, and 1980 for reviews). The insects, with their monopoly on true flapping flight, spectacular mass migrations with seasonal returns (Urquhart 1960; Hagen 1962; Rainey 1978), and status as crop pests, have received the most attention. However, other groups of terrestrial arthropods also migrate (Southwood 1962). The most impressive mass migrations of non-insect taxa are those of the spiders, which "balloon" on long buoyant strands of silk. Episodes of such so-called "aeronautic behavior" are often regional in scope and leave the countryside festooned with spent silken "gossamer" (Comstock 1948).

The timing of migratory movements may correspond to climatic events. For example in spiders aeronautic behavior peaks sharply during periods of unseasonably warm and balmy weather which produces ideal conditions for lifting the animals into swiftly moving air layers. However it is generally agreed that the tendency to migrate is a fixed rather than a facultative response to the immediate abiotic or biotic environment (Johnson 1960; Kennedy 1961; Southwood 1962, 1977; Dingle 1972). The major selective factor in the evolution of migratory behavior is presumed to be the predictability (defined below) of the habitat, with habitat unpredictability favoring migratory behavior. If this "habitat predictability hypothesis" is correct, the intensity or frequency of migratory behavior should decrease as the predictability of the habitat increases.

In the only study of spiders that bears directly on the hypothesis, Richter (1970) determined the ballooning frequencies of spiderlings of eight Dutch species of the wolf spider genus Pardosa (Lycosidae) in relation to published information on the abundance (i.e., commonness) and "stability" (both designated as low, intermediate, or high) of their typical habitats in Britain. My analysis of his data indicates that ballooning frequency is significantly inversely correlated with habitat abundance but not with habitat stability. Unfortunately his populations were not sampled from the habitats described and there are uncertainties about the assignment of levels of stability.

Concepts of stability and predictability are central to various areas of ecological theory but have only recently been rigorously defined. Predictabil-

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*Matthew H. Greenstone is an Assistant Research Scientist in the Department of Entomology and Nematology, University of Florida. The research reported here was performed while he was a Lecturer in the Department of Ecology and Evolutionary Biology, University of California, Irvine. His principal research interests include spider evolutionary ecology and the application of serological methods to arthropod ecology. Current address: Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611.

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ity may be thought of as comprising two components, constancy and contingency (Colwell 1974), which are nicely illustrated by rainfall in Mediterranean climate regions. These regions are characterized by rainy winters and largely rainless summers. In such areas rainfall has low constancy (because it doesn't always rain in all seasons) but fairly high contingency (because the presence and absence of rainfall are contingent on season, although the exact month of onset or cessation of rains may vary from year to year). Thus rainfall has moderate predictability in Mediterranean climates, with constancy intermediate and contingency higher than for most other temperate climates.

The predictability of rainfall is a major determinant of habitat predictability for some animals. Although all wolf spiders (Araneae: Lycosidae) require free water for drinking (Parry 1954), differences in lifestyle alter the effect of rainfall on habitat predictability for the two species studied here. *Pardosa ramulosa* (McCook) and *Pardosa tuoba* Chamberlin are closely related species that are sympatric over much of their ranges in California (Vogel 1970). *P. ramulosa* is highly specialized in both diet and foraging mode, feeding on aquatic insects that it plucks from the surface of standing water (Greenstone 1979, 1980). In the San Francisco Bay region, which has a Mediterranean climate, it inhabits the banks of fresh- and saltwater pools, some of them small, isolated, and seasonal. In the same region, *P. tuoba* is found in extensive coastal prairie and scrub habitats, where it feeds on terrestrial insects (Greenstone 1980). Because *P. ramulosa* requires standing water, its habitats tend to be less predictable than those of *P. tuoba*, to the extent that *P. ramulosa* has to retire from some habitats during the dry season while *P. tuoba* can remain active throughout the year (Greenstone 1980, Table 1).

The two species' habitats are in many cases adjacent and even nested (Greenstone 1980), permitting a test of the habitat predictability hypothesis in the absence of confounding climatic or other geographic variables. If the hypothesis is correct *P. ramulosa* should have a higher ballooning frequency than *P. tuoba*.

**Methods**

Egg-case-bearing females of both species were collected in April and May of 1978, *P. tuoba* from coastal prairie habitats in Point Pinole Regional Park and Jewel Meadow in Tilden Regional Park, and *P. ramulosa* from the margins of pools in Point Pinole Regional Park, Jewel Meadow, and the Petaluma Marsh (refer to Greenstone 1980 for complete habitat and locality descriptions). The animals were maintained in the laboratory until the spiderlings had hatched and dispersed from their backs. Each spiderling was then transferred to its own 25 X 95 mm cotton-plugged shell vial, with moisture provided by a distilled water-saturated cotton ball at the bottom and a 3 mm diameter wooden applicator stick as a dry perch.

Ballooning behavior was assayed with an apparatus similar to that of Richter (1967, 1970) (Fig. 1). Spiderlings were placed in groups of 4 or 5 on the tips of individual 5 mm diameter dowels in the air stream of a variable speed electric fan directed upward at an angle of 45 degrees. Heat and illumination were provided by a 250 watt incandescent lamp suspended 20 cm above the dowel tips, and temperature and wind speed were monitored.
Fig. 1. Apparatus used in ballooning assays. Note thermocouple probe among dowel tips and anemometer probe just to the right of the dowels. Clock timer was used to time periods of wind and calm.
with thermocouple and hot-wire anemometer probes mounted near the spiderlings. All trials were run at a windspeed of 1.0 m/s and a temperature of 27-28°C, which are in the optimum range for other _Pardosa_ species (Richter 1970). Each animal was fed one adult vestigial-winged _Drosophila melanogaster_ before its ballooning trial.

Because intermittent air movements are more effective than continuous ones in eliciting ballooning behavior in _Pardosa_ species (Richter 1967), each spider was observed during five 2-minute periods of wind separated by 1-minute periods of calm. An animal was scored as a ballooner only if it ballooned or exhibited “tip-toe” behavior, which normally precedes ballooning (Richter 1970). Only second instar spiderlings (hatchlings) were tested since they are more apt to balloon than older animals (Richter op. cit.). Ninety-one _P. tuoba_ and 235 _P. ramulosa_ spiderlings were tested.

**RESULTS AND DISCUSSION**

The proportions of ballooners in the two species were .032 (3/91) for _P. tuoba_ and .098 (28/285) for _P. ramulosa_. These proportions are highly significantly different (G = 22.638, p<<.001, log-likelihood ratio test, Sokal and Rohlf 1969).

The results were in the expected direction and support the habitat predictability hypothesis. What are the broader implications of the results? On a purely local level they may explain the absence of _Pardosa tuoba_ from Neil’s Island, a collecting locality with typical _P. tuoba_ habitat (Greenstone 1980, Table 1). Neil’s Island is a true ecological island, comprising coastal prairie, savannah and woodland habitats and entirely surrounded by estuarine salt marsh. Since _P. tuoba_ is never found in salt marsh, the only way it could get to Neil’s Island is by ballooning, which it does with low frequency. Any arriving aeronaut would have to survive six or seven molts to reach adulthood and locate a mate in order to reproduce. Furthermore the relatively small size of the island may promote high extinction rates for any populations that do manage to get established (MacArthur and Wilson 1967).

Ballooning, like other modes of arthropod migration, has broad theoretical and practical implications. Both natural and managed habitats are distributed in time and space with varying degrees of predictability, and the existence of migration and diapause phenomena in terrestrial arthropods attest to strong selection for tracking habitats in space and time. Because a major aim of these symposia is the application of basic research to the solution of practical problems (Lloyd 1981) I shall confine my remaining remarks to a consideration of the possible practical implications of ballooning.

The relevance of ballooning to agriculture is evident given the variety of spatial and temporal patterns in planting and harvest. Annual crops may appear and disappear within and between regions with greater or lesser spacing and regularity, while perennial crops tend by their nature to be more predictable to their arthropod inhabitants (Ehler 1977). Though some thought has been give to the movement of arthropod pests within this habitat mosaic (Rabb and Kennedy 1979; Stimac 1982, this Symposium), little has been given to the movement of their natural enemies. Spiders are the most numerous and effective predators in some agricultural situations, especially fruit orchards and rice fields (Kenmore 1980; Mansour et al.
1980; Kiritani 1976). Pest management schemes designed to disrupt pest populations might also make it difficult for spiders to remain associated with those populations. For example, the spacing or timing of crops might be manipulated to discourage pest movements from field to field, or stubble might be burned to destroy diapausing immature stages of the pest. In such cases spider species from less predictable habitats with greater ballooning frequencies could be artificially introduced. Alternatively, resident species that are otherwise well-adapted to the pest and its habitat could be reared in the laboratory, selected for higher ballooning frequency, and returned to the field; lower-frequency ballooning populations could be selected for perennial crops. This scheme is of course contingent on ballooning tendency having high heritability, which is an implicit assumption of the habitat predictability hypothesis.

The quantitative study of ballooning is in its infancy. The only other studies comparable to mine are those of Richter (1967, 1970), which also involve wolf spiders. This is unfortunate because lyosids make up relatively little of the aeronautil fauna, which is dominated by the Linyphiidae (Bristowe 1939; Duffey 1956). The linyphiids are unique, because with the exception of a few tiny species in other families (Horner 1974), they are the only spiders small enough to balloon as adults as well as juveniles. This means that they have survived most pre-reproductive mortality at the time of ballooning and therefore have higher reproductive value and colonizing potential than do juveniles (MacArthur and Wilson 1967). Since linyphiids are known to be key predators in some crop systems (Kenmore 1980; Yamanaka et al. 1972), knowledge of their ballooning biology may enable us to raise their effectiveness as natural enemies, besides adding a new dimension to our basic understanding of spider migration.

**Summary**

Spiders disperse by “ballooning” on long buoyant strands of silk. The hypothesis that habitat unpredictability selects for high ballooning frequencies of spiderlings was tested by comparing two wolf spider species with populations in adjacent and nested Northern California habitats. *Pardosa tuoba* is active throughout the year in coastal prairie and scrub habitats where it feeds on terrestrial insects, while *P. ramulosa* is a specialist on aquatic insects and requires open water to feed. Because the availability of open water is somewhat unpredictable in Northern California, *P. ramulosa* has a less predictable habitat than *P. tuoba*. *P. ramulosa* was found to have the higher ballooning frequency, as predicted by the hypothesis. These results are relevant to a consideration of the role that spiders might play in pest management schemes which make use of various spatial and temporal cropping regimes.

**Appendix**

1. Abundance: r = 0.844, p < .01; Stability: r = 0.172, p > .10 (Spearman Rank Correlation Coefficient, Siegel 1956).
2. Predictability and its components have been computed for coastal California (Malaurie 1976) using 25 years of rainfall data, and show predictability and constancy lower than three subtropical to tropical and one tem-
perate site, and contingency equivalent to that of a tropical site having pronounced wet and dry seasons (Colwell 1974).

*Ballooning is not unique to spiders, being known also from various Lepidopterous larvae, including forest pests such as Gypsy Moth (*Porthetria dispar*) (Leonard 1970) and Spruce Budworm (*Choristoneura fumiferana*) (Wellington and Henson 1947).

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LITERATURE CITED


