Scale of Recruitment Limitation in the Western Harvester Ant (Hymenoptera: Formicidae)

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ABSTRACT We examined the scale of recruitment limitation in the western harvester ant, *Pogonomyrmex occidentalis* (Cresson). We measured colony density of 98 plots (0.25 ha) over an area of 500 ha. By applying an interpolation/extrapolation analysis to the spatial variability in colony density, we were able to accurately identify the location of two mating swarms. These two swarms were ≈1,400 m apart. Consequently, we conclude that if recruitment limitation generates variability in ecological processes such as density dependence, then variability should occur on the order of 1.5 km.

KEY WORDS Western harvester ants, ants, recruitment limitation, *Pogonomyrmex*

THE INTERPLAY BETWEEN dispersal of young and variation in postdispersal mortality due to habitat heterogeneity is important to understanding population regulation in open systems (Roughgarden et al. 1985). Populations are considered open when there is considerable variability in the quality of habitat, and individuals are capable of dispersing into different habitat types (Hixon et al. 2002). There is strong empirical evidence that patterns of recruitment are important to population densities in a number of systems (Victor 1986, Roughgarden et al. 1988, Jones 1990, Doherty and Fowler 1994, Hubbell et al. 1999, Cole and Wiernasz 2002).

In recruitment-limited systems, the patterns of juvenile dispersal generate patterns of spatial variability in population densities that depend upon postrecruitment mortality and the physical factors determining recruitment. In some cases, variability in postrecruitment mortality will obscure the recruitment signal, and mortality rates will be the primary factor determining spatial variability in abundance (Roughgarden et al. 1985, Steele and Forrester 2002). Alternatively, recruitment can have large transient effects on populations. In coral reefs, the populations of some fish species are dominated by cohorts produced in a year of high productivity (Victor 1983, Doherty and Fowler 1994, Caley et al. 1996). When factors that determine relative levels of recruitment remain constant between years, recruitment-limitation should generate predictable and consistent landscape variation in population densities, even in long-lived organisms.

The extent to which recruitment patterns will be spatially consistent from year to year will depend upon the factors determining patterns of recruitment. In both marine and intertidal systems ocean currents are the primary factor that determines where passively dispersing larvae settle (Victor 1986, Roughgarden et al. 1988). Although ocean currents do vary, Doherty and Fowler (1994) reported some temporal consistency in recruitment in damselfish over 10 yr in the southern Great Barrier Reef.

In the western harvester ant, *Pogonomyrmex occidentalis* (Cresson), where recruitment limitation has been documented, the location of mating swarms is the primary factor determining local population densities (Cole and Wiernasz 2002). Newly mated queens are more likely to settle close to the mating swarm. Consequently, recruitment tends to be relatively high close to mating swarms (Cole and Wiernasz 2002). Because mating swarms occur on high points in the landscape and those high points are the same from year to the next, recruitment limitation should generate interesting spatial variation in patterns of colony density. However, *P. occidentalis* colonies can live as long as 45 yr (Keeler 1993), allowing postrecruitment mortality to wash out the recruitment signal.

We examined whether large-scale patterns of colony density of *P. occidentalis* are determined by site topography. At our study site, Cole and Wiernasz (2002) demonstrated that on a 50-ha scale, colony density is a function of distance from a single hilltop on which mating swarms consistently form. Here, we further test the recruitment limitation hypothesis by asking whether on the scale of ≈500 ha the location of mating swarms can be predicted based on spatial variation in colony densities in 98 plots (50 by 50 m). By extending the spatial scale of this study, we are able to test whether the previous finding was due to an unusually important mating site, or rather, whether spatial variation in relation to mating swarms is a general feature of this system. Additionally, by expanding this study beyond the scale of a single mating location, we were able to determine the scale on which population densities can be expected to vary in *P. occidentalis.*

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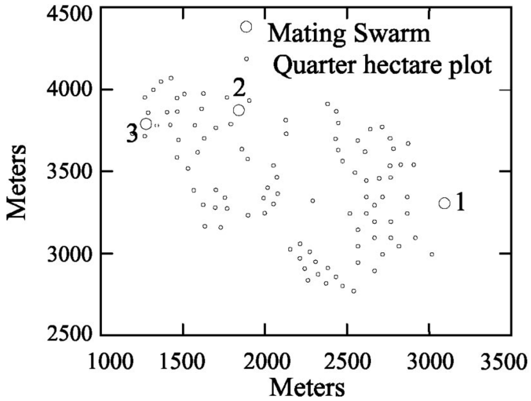

Fig. 1. Small circles are the centers of the 50 by 50-m plots. We visually surveyed the number of colonies in each of 98 plots. The positions of the three major swarms referred to in the text are shown with numbered, large circles.

Materials and Methods

We conducted the study on Bureau of Land Management land ≈15 km northwest of Fruita (Mesa County), CO (39° 16′N, 108° 45′W), at 1,470-m elevation. The soil is alkaline clay with seleniferous patches. The plant community includes saltbrush (*Altriplex* spp.), *Gutierrezia sarothrae* (Pursh), *Bromus tectorum* L., *Tetradymia spinosa* (Hooker & Arnott), *Hilaria jamesii* (Torrey), and *Oryzopsis hymenoides* (Roemer and Schultes).

P. occidentalis queens and males form mating swarms on high points in the landscape after rains in late summer. The location of these swarms is largely consistent from 1 yr to the next, although swarms do not form at all locations every year. Upon dispersing from the swarm, single queens initiate colonies that can grow up to 20,000 workers and may live 45 yr (Keeler 1993).

We laid out 98 plots (50 by 50 m) haphazardly over roughly a 1.5 by 1.5-km area (Fig. 1). Efforts were made to lay plots in relatively flat areas and to minimize the area of steep embankments within plots. This meant that areas of strong relief were unsampled. We mapped the corners of the plots to within 0.03 m by using a Leica TC600 Total Station and calculated the locations of the plots based on their center points. Twenty of the plots are part of a long-term observational study at the site. Fifty-three plots are part of other experiments that did not affect colony densities in the plots. Initial analysis of 72 of the plots suggested the presence of a swarm outside the area covered by those 72 plots. We laid out the final 25 plots in the general vicinity of the swarm suggested by those initial analyses.

We visually surveyed colony density in all plots. We counted all colonies in the 20 plots from the long-term observational study in 1996. We surveyed 52 of the plots in 1997 and 1998 (one of 53 plots was only surveyed in 1998) and the final 26 plots in 1998. Mature colony density is highly correlated from year to year because of the long-lived nature of colonies and the relatively low levels of colony recruitment, even in productive years (Billick et al. 2001). Thus, surveying the plots in different years had little impact on our ability to detect areas of high colony density.

Cole and Wiernasz (2002) previously developed a spatial analysis to determine the relationship between colony density and the location of mating swarms. This technique was based on a specific biological model that local colony density is higher closer to swarms. Specifically, using a program written in TrueBasic, we calculated the correlation coefficient between colony density and distance from different positions at the site. We excluded locations from the analysis if <24 plots were within a neighborhood size of 800 m to avoid artifacts due to small samples. Using the coordinate system in Fig. 1, and ranging on the x-axis from 657 to 3,424 m and on the y-axis 2,237 to 4,606 m, at every 50-m interval we calculated the distance to all 0.25-ha plots within 800 m of that point. We then calculated the correlation coefficient between distance from that point and colony density. We used the correlation coefficient because it provided a convenient standardized scale that ranged from −1 to +1. "Hot spots" show up on the landscape as large, negative correlation coefficients; as one moves away from those locations, colony density declines.

We chose a neighborhood size of 800 m as a compromise between having too small a neighborhood size and having too large a neighborhood size. If the neighborhood size was too small then there would not be 24 plots within most distances on our grid to calculate a correlation coefficient. If the neighborhood size was too large then multiple swarms would be present within the neighborhood of a given point and the effect of any particular swarm on colony density could not be determined. A neighborhood size of 800 m also has biological significance because 800 m is the estimated distanced that queens move (Cole and Wiernasz 2002). We performed sensitivity analyses where we varied the neighborhood size from 400 to 2,200 m, in increments of 200 m. Changing the neighborhood size from 400 to 1,200 m did not affect identification of the location of hot spots. Once the neighborhood size exceeded 1,200 m, however, there were essentially no hot spots; no locations on the grid were associated with high local densities of colonies.

We visualized these data using Systat to generate a two-dimensional contour plot of the regression values. This contour map allowed us to determine the number and location of hot spots in colony density and then to qualitatively assess whether the position of those hot spots corresponded to locations where swarms were known to occur.

We located the actual swarms on the site by direct observation. We identified the locations of two swarms by surveying all high topographic points on the day after the mating flight in 1998. High points with an abundance of dead males were assumed to have had a mating swarm. We mapped the locations of mating swarms using the Leica TC600 Total Station.

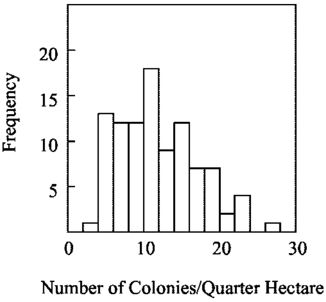

Fig. 2. Frequency distribution of the density of colonies on the 0.25-ha plots ($N = 98$).

Although there are a number of different types of spatial analyses that could be used to analyze the relationship between mating swarms and patterns of colony density, this "regression" approach has a number of methodological advantages. First, because it replicates the approach of Cole and Wiernasz (2002) on a larger scale, it directly tests the generality of those findings and asks whether the results can be repeated in a different context. Additionally, this type of "averaging" approach, where the value of any one location is based upon the values of neighboring areas, makes it possible to estimate values for plots in which measurements were not made and also helps reduce "noise," or variation in local density that is related to local, as opposed to regional, effects. Finally, as mentioned previously, this approach is based directly on a model of the biological process in question.

Results

Colony density on the 0.25-ha plots averaged 12.5 colonies with a standard deviation of 5.3. Figure 2 displays a frequency distribution of colony densities. The distribution was slightly non-normal, with a right skew (G1 = 0.51, SE = 0.24, $P < 0.05$, *t*-test) and no evidence of significant kurtosis (G2 = −0.36, SE = 0.48, $P > 0.4$, *t*-test).

Our interpolation procedure generated correlation coefficients for 1,402 of the 2,377 locations on the grid that had at least 24 plots within an 800-m radius. For a random location within the grid colony density tended to increase with density from location; the mean correlation coefficient of colony density on distance was 0.027 (SE = 0.0074, $P < 0.0001$, $n = 1{,}402$). This distribution was also slightly non-normal. Although there was no evidence of a significant skew (G1 = 0.11, SE = 0.065, $P > 0.05$, *t*-test), there was evidence of significant platykurtosis with more intermediate values than expected for a normal distribution (G2 = −0.81, SE = 0.13, $P < 0.0001$, *t*-test).

Three swarms were located during the survey in 1998 (Fig. 1). When we used Systat's 2D contour algorithm to spatially visualize the correlation coefficients, we found two mating swarms where colony density within plots declined with increasing distance of plots from those swarms (Fig. 3). The location that demonstrated the strongest negative relationship between distance and colony distance corresponded to swarm 1 (a large negative correlation coefficient indicates that colony density is high in vicinity of the point). Swarm 1 fell within the contour line of −0.5. The smallest calculated correlation coefficient was −0.58, and 27 locations had correlation coefficients less than −0.5, all within this region. The second location that seemed to be a hot spot corresponded to swarm 2. This swarm fell within the contour line of −0.30. The smallest calculated correlation coefficient in this region was −0.38. Figure 4 shows the position of the 128 locations that had correlation coefficients less than −0.35. The bulk of these locations were associated with the first hot spot; there were only seven locations outside the region of the first hot spot and given the scale of our sampling and analysis, these locations directly overlapped the second swarm. There was no evidence that the third swarm was associated with high local densities of colonies.

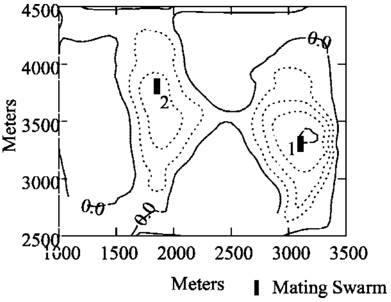

Fig. 3. Contour diagram of the correlation coefficients. The first and second swarms are the labeled dark rectangles. Only negative contours are shown. The zero contour is depicted with a solid line and is labeled with 0.0. Contour lines represent increments of 0.15 (0, −0.15, −0.30, and −0.45), except for the −0.50 line, which is the solid line partly overlapping the first swarm. Low negative values in the landscape represent hot spots of locations where colony density increases with increasing proximity to that location. Contours were generated with Systat's contour algorithm and represent "smoothed" values.

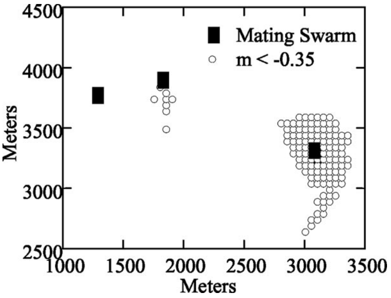

Fig. 4. Location of the 128 points on the grid that had correlation coefficients less than −0.35. These locations are represented as open circles. Unlike in Fig. 3, this figure shows actual (not smoothed) values. Locations of the three swarms are shown with large, dark rectangles.

Discussion

This study demonstrates that the location of mating swarms can be predicted based upon patterns of colony density. Additionally, this finding demonstrates that the effects of recruitment limitation are evident in patterns of colony densities on large spatial scales. Interestingly, spatial variation of colony density failed to predict the presence of one of the three swarms located onsite in 1998, swarm 3. Indeed, in this study area, swarms have been observed in eight distinct locations over the past several years. Because *P. occidentalis* colonies are long-lived, reaching ages >40 yr, a "recruitment signal," where colony density declines with increasing distance from the location, should only be apparent in areas that consistently have large swarms. Spatial variability in colony density should indicate locations where important swarms tend to occur year after year. The lack of an effect of the location of swarm 3 on surrounding colony densities suggests that mating swarms do not consistently occur on this site.

The distance between the two hot spots of high local colony density associated with swarms of ≈1,400 m, suggesting that the scale of spatial variation in colony densities will be on the order of 1.5 km. Patterns of maximum queen flight distances are consistent with this interswarm distance. Maximum queen flight distances in *P. occidentalis* are on the order of 800 m (Cole and Wiernasz 2002). The number of dispersing queens seems to decline linearly with distance from the swarm. Some areas of the site do not receive enough queens to saturate the site, given a distance of 1,400 m between major swarms. If the swarms were significantly closer, then all locations would receive an "excess" of queens, rendering recruitment limitation unimportant and eliminating any recruitment signal.

The presence of two persistent swarms of sufficient distance apart to generate recruitment limitation could be either the chance consequence of the geography of the site, or it could be a natural result of the mating system. The most attractive mating sites, e.g., hills that clearly stand out on the horizon, could simply be far apart at this site. If interswarm distance is a function of geography, then recruitment limitation will not be important in locations that have attractive mating sites more densely distributed. Alternatively, recruitment limitation may naturally arise as the by-product of the mating system. There may be strong selection for queens to find the largest mating swarm within their flying range. Queens that choose smaller swarms may be at a disadvantage because they run the risk of going unmated or of mating with males from the same colony. Indeed, queens that receive few matings are at a serious fitness disadvantage (Cole and Wiernasz 1999). Consequently, swarms may naturally form at distances that are relatively far apart given the dispersal distances of mated queens. If distances between swarms are commonly large relative to queen dispersal distances because of selection on queens to find large mating swarms, then recruitment limitation will not depend upon the fortuitous placement of attractive locations for mating swarms but should be common over the entire range of *P. occidentalis.* In this case, recruitment limitation might be a self-organizing feature resulting from a combination of mating aggregations and selection for multiple matings.

The distance of 1,400 m between hot spots provides perspective on the scale on which ecological processes that depend upon local colony density should vary. At this site, the importance of established colonies to inhibiting new colony recruitment varies spatially (Billick et al. 2001). In a previous study, when all adult colonies were removed, recruitment increased in two locations but not in a third location. Spatial variability in the importance of density dependence to recruitment can be explained by spatial variation in recruitment. Areas relatively close to swarms receive sufficient numbers of dispersing queens such that colony densities reach saturation (Cole and Wiernasz 2002); adult colonies are common enough to inhibit new colony recruitment. Alternatively, established colony densities may not be sufficiently high in areas that receive few dispersing queens to have a noticeable effect on colony recruitment. Thus, spatial variation in recruitment generates spatial variation in colony density and the intensity of intraspecific competition. The interswarm distance of 1,400 m in this study indicates that the importance of density dependence will vary on a spatial scale of hundreds of meters.

Warner and Hughes (1988) suggest that recruitment limitation will be difficult to detect in long-lived organisms because spatial variability in recruitment over the years will obscure any single recruitment event. Our study demonstrates the opposite. Recruitment limitation is observable primarily because colonies are long-lived. Although each year there are minor swarms whose location may be largely unpredictable, the recruitment signals associated with those swarms make no lasting impact on colony density. Instead, swarms that are consistently present and large determine much of the spatial variability in colony density and emerge over the long-term. These results suggest that in recruitment-limited systems spatial analysis of population densities can be used to make predictions concerning a range of ecological phenomena, including the biology of reproduction and dispersal, as well as the strength of intra- and interspecific competition.

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