Dispersal dynamics: Distribution of lady beetles (Coleoptera: Coccinellidae)

VLASTIMIL KRIVAN

Department of Theoretical Ecology, Institute of Entomology, Biology Centre, Academy of Sciences of the Czech Republic, Branišovská 31, 370 05 České Budějovice, Czech Republic; e-mail: krivan@entu.cas.cz

Key words. Balanced dispersal, Coccinella septempunctata, habitat choice, ideal free distribution, matching principle

Abstract. This article studies coccinellid dispersal in heterogeneous environments using some hypotheses on dispersal rates that correspond to empirical observations. It is assumed that emigration rates increase with decreasing patch payoff that is measured either as the number of aphids per a lady beetle, or as the number of aphids only. Three scenarios for immigration are considered: individuals choose patches unconditionally, immigration is proportional to patch quality, and immigration is proportional to patch payoff. Coccinellid spatial distributions corresponding to these assumptions are given by a power law. Using some data from the literature on distribution of Coccinella septempunctata it is shown that the model with emigration proportional to the ratio of the number of conspecifics to aphid density and unconditional immigration rates provides the best fit when compared with the other models. This model predicts undermatching where better patches get lower consumer density when compared with the ideal free distribution.

1. INTRODUCTION

Distribution of consumers with respect to their resources is important for understanding mechanisms regulating species coexistence. Several authors observed (e.g., Turchin & Kareiva, 1989; Hodek & Honěk, 1996; Elliott & Kieckhefer, 2000; Osawa, 2000; Evans & Toler, 2007) that density of adult lady beetles is positively correlated with aphid density. The question arises about what are the mechanisms that create such correlated distributions. To answer this question the two components that describe animal dispersal, immigration and emigration, must be known.

There is empirical evidence that the time coccinellids remain in experimental plots is positively correlated with patch quality. Banks (1957) and Osawa (2000) observed that lady beetles spend more of their time searching where prey are dense than where prey are sparse. Ives et al. (1993) observed positive correlation between the time females of lady beetle stayed on a fireweed (Epilobium angustifolium L.) stem and aphid density. These authors also observed a similar relationship on a larger spatial scale where scattered individuals of fireweed were manipulated experimentally to harbor varying numbers of aphids. Van der Werf et al. (2000) observed increased residence time and 10–20 times higher abundance of lady beetles in sugar sprayed plots when compared with control plots. As the emigration rate is inversely proportional to the staying time, these works (reviewed in Evans, 2003) provide solid evidence that emigration rate decreases with increasing number of prey. Cardinale et al. (2006) observed a linear negative relationship between the emigration rate of lady beetles and the logarithm of aphid density. However, even when aphids are abundant at a given habitat a significant proportion of coccinellid adults disperses every day (Ives, 1981; Frazer, 1988). Interference between conspecifics can be one of the reasons for dispersal. For example, Růžička & Zemek (2007) observed that coccinellid larvae avoid staying on substrates with tracks of other larvae. These observations suggest that emigration rate may depend on both aphid and conspecific density.

With respect to immigration the situation is less clear. Honěk (1980) (see also Hodek & Honěk, 1996) estimated that the minimum aphid abundance capable of retaining predators is about 10 aphids per square meter of the crop area. Tracking individual lady beetles Osawa (2000) showed that short range movement of a lady beetle within plants of the same species or genus led to a better habitat only in approx. 44% of observed cases. However, movement between different sub-populations (i.e., plants of different genus) led to a better habitat in 75% of observations. Cardinale et al. (2006) observed no correlation between immigration rates and aphid density.

An idealized model describing spatial distribution of consumers in a patchy environment is the Ideal Free Distribution (IFD; Fretwell & Lucas, 1970). At the IFD, consumer payoff in all occupied patches is the same and the number of immigrants to a given patch must equal the number of emigrants from the patch. Such a pattern of equalized immigration and emigration is called “balanced dispersal” (McPeek & Holt, 1992; Doncaster et al., 1997; Holt & Barfield, 2001). As under the IFD number of consumers does not equalize across patches, it is clear that to keep such distribution the probability that an individual from a patch with many conspecifics will disperse must be smaller than is the same probability for an individual in a less densely populated patch. In fact, under balanced dispersal, there is an inverse relation between local population size and per capita dispersal rate so that individuals at good sites are less likely to disperse than those from poor sites (Holt & Barfield, 2001). Unbalanced dispersal caused by e.g., random animal movements between
patches leads to a higher consumer density in poor patches and a lower density in good patches when compared with the IFD. This phenomenon is known as “undermatching” (Milinski, 1988; Kennedy & Gray, 1993; Houston et al., 1995; Jackson et al., 2004). It was shown that unconditional (i.e., random) dispersal should be selected against in spatially heterogeneous environments (Hastings, 1983; Holt, 1985; McPeek & Holt, 1992).

The Fretwell and Lucas concept is static in the sense that it does not address the question how a population distribution achieves the IFD. Cressman & Křivan (2006) studied various dispersal dynamics that lead to the IFD. They proved that if individuals never move to patches with a lower payoff and they do not ignore the best patch then the resulting distribution will correspond to the IFD. In this article I will study dispersal rules that are qualitatively consistent with empirical observations on coccinellids. Using some empirical data on lady beetles distribution I will test which of these dispersal rules leads to a distribution that fits the data best.

2. MODELS

In this section I construct models that describe predator dispersal in a heterogeneous environment consisting of \( H \) patches. Following Cressman & Křivan (2006), consumer distribution dynamics are described by

\[
\frac{dC}{dt} = \sum_{j=1}^{H} \left( I_j(m) m_j - I_j(m) m_i \right) \quad \text{for } i = 1, \ldots, H. \tag{1}
\]

Here \( I_i \) is the transition probability that an individual currently in patch \( j \) disperses to patch \( i \) in a unit time interval. By choosing a small enough unit time interval, I will assume that all entries in the dispersal matrix are non-negative and sufficiently small so that \( 1 - \sum_{i=1}^{H} I_{ij} > 0 \). Because the terms \( I_j(m) m_j \), describing movement from patch \( i \) to itself cancel in model (1), diagonal terms of the dispersal matrix \( I \) can be chosen in such a way that the sum of the entries in each column of the migration matrix equals 1 (by setting \( I_j(m) = 1 - \sum_{i=1}^{H} I_{ij} \)). Moreover, I will assume that \( I_i \) is the product of immigration rate \( a_i(m) \) to patch \( i \) and emigration rate \( b_i(m) \) from patch \( j \). This means that emigration from a patch and immigration to a patch are assumed to be independent processes. These assumptions lead to the following form of migration dynamics

\[
\frac{dC}{dt} = a_i(m) \sum_{j=1}^{H} b_j(m) m_j - b_i(m) m_i \sum_{j=1}^{H} a_j(m) \quad \text{for } i = 1, \ldots, H. \tag{2}
\]

The first term on the right hand side describes immigration to patch \( i \) and the second term emigration from patch \( i \). The equilibrium distribution \( m^* = (m_1^*, \ldots, m_H^*) \) of model (2) satisfies the following equation

\[
\frac{a_i(m_i^*)}{b_i(m_i^*)} = C \quad \text{for } i = 1, \ldots, H \tag{3}
\]

where constant \( C \) is given by

\[
C = \frac{\sum_{j=1}^{H} a_j(m_j^*)}{\sum_{j=1}^{H} b_j(m_j^*)}. \]

Cressman & Křivan (2006) proved that provided dispersal matrix changes continuously with changing distribution and that immigration to a patch does not decrease as a payoff in that patch increases and emigration from a patch does not increase as the payoff in that patch increases then the equilibrium distribution is locally asymptotically stable. These assumptions hold for all dispersal models I will consider below.

2.1 Patch payoff

I will assume that each patch is characterized by its payoff \( V_i \) and I will consider two payoff functions. The first payoff is given by patch quality (measured as aphid abundance \( K_i \) in the patch) per an individual lady beetle

\[
V_i = \frac{k_i}{K_i}. \tag{4}
\]

Because under the IFD payoffs in all occupied patches must be the same (Fretwell & Lucas, 1970), payoff (4) leads to the so called “matching principle”

\[
\frac{m_i}{m_j} = \frac{K_j}{K_i} \quad \text{for } i, j = 1, \ldots, H
\]

(e.g., Parker, 1978, Parker & Stuart, 1976, Milinski & Parker, 1991, Sutherland, 1996). Thus, input matching principle is a particular form of the IFD for patch payoffs given by (4). I remark that under the input matching principle all patches will be occupied by lady beetles because as the consumer numbers in a patch decrease patch payoff tends to infinity and individuals start to move there.

As an alternative, I will also consider the case where patch payoff does not depend on the number of conspecifics, i.e.,

\[
V_i = K_i \tag{5}
\]

In this case, under the IFD only the patch(es) with the highest \( K \) will be occupied. This shows why payoff (4) is preferred to (5) in the literature on the IFD.

2.2 Emigration

Ives et al. (1993) and Osawa (2000) observed that the patch staying time of a lady beetle increases with aphid density. Here, I will generalize this observation by assuming that the staying time increases linearly with patch payoff (the proportionality constant cancels out in subsequent calculations and I set it arbitrarily equal to 1). As the emigration rate from the \( j \)-th patch is inversely proportional to patch payoff (i.e., \( b_i = \frac{c}{V_i} \)) I get

\[
b_i = \frac{c}{V_i} \tag{6}
\]

when \( V_i \) is given by equation (4) and

\[
b_i = \frac{1}{K_i} \tag{7}
\]

when \( V_i \) is given by (5). In both cases, emigration rates from patch \( i \) always decrease with increasing number of aphids in that patch.

2.3 Immigration is unconditional

Here I assume that the probability of immigrating to any of the \( H \) patches is the same and equal to \( a_i = 1/H \) (assuming that animals can return to the patch they departed from). From (3) it follows that for emigration rates given by (6) the equilibrium distribution satisfies

\[
m_i = c K_i \quad \text{for every } i = 1, \ldots, H \tag{8}
\]

where \( c \) is a constant. Thus, \( m_i/m_j = \sqrt{K_j}/K_i \) which is not the IFD. Unconditional immigration leads to “undermatching” where better patches get lower animal numbers when compared with the IFD.

For emigration rates (7) that depend on the aphid density only the equilibrium distribution is

\[
m_i = c K_i \quad \text{for every } i = 1, \ldots, H. \tag{9}
\]

It is interesting to note that despite the fact that immigration is random and emigration rates depend on the patch quality only, the resulting lady beetle distribution corresponds to the Parker’s matching principle, thus to the IFD.
First, I will consider results for emigration rates given by (6). The corresponding distributions are then given by models (8), (9) and (11). Among these models, model (8) that corresponds to unconditional immigration (solid line in Fig. 1) fits the data best (in the sense of mean sum of squares, Table 1) while model (9) that corresponds to the IFD provides the worst fit (dotted line in Fig. 1).

Second, when emigration rates are given by (7), the corresponding distributions are given by models (9) and (10) because the model with unconditional immigration and the model with immigration proportional to patch payoff lead to the same distribution (9). Model (10) gives even worse fit (long-dashed line) than model (9).

In addition, I also estimated parameters for a general power function $m_i = cK_i^d$. Not surprisingly, the general power law with two estimated parameters $c = 4.3$ and $d = 0.435$ gives the best least-squares fit (dot-dashed line in Fig. 1, mean sum of squares = 1580).

### 4. DISCUSSION

In this article I studied animal dispersal using some hypotheses on dispersal rates that correspond to empirical observations on coccinellids. I assumed that emigration rates increase with decreasing patch payoffs defined either as the ratio between patch quality (measured by the number of aphids) and number of consumers, or as the patch quality only. It was observed in several studies on coccinellids that emigration rates increase with decreasing patch quality (Ives et al., 1993; Hodek & Honěk, 1996; Honěk, 1982).
Osawa, 2000; Cardinale et al., 2006). It was also observed that searching efficiency decreases with increasing number of conspecifics (Siddiqui et al., 1999).

For immigration rates, I considered three scenarios: individuals chose patches unconditionally, immigration is proportional to patch quality, and immigration is proportional to patch payoff. These assumptions allowed me to make predictions on consumer distribution. All resulting distributions are given by a power law. Using data on distribution of Coccinella septempunctata with respect to various aphid densities taken from Honěk (1982) (see also Hodek & Honěk, 1996) I tested which of these models fits the data best. Among six different patterns of dispersal studied in this article, the model where emigration is directly proportional to number of conspecifics and inversely proportional to number of aphids combined with unconditional immigration fit data from Honěk (1982) best (solid line in Fig. 1). This model corresponds to the so called “undermatching” where poor (good) patches contain higher (lower) proportion of C. septempunctata than would correspond to the IFD. This phenomenon was observed in several studies on animal distribution (e.g., Milinski, 1988; Kennedy & Gray, 1993; Houston et al., 1995; Jackson et al., 2004). Honěk’s data on lady beetles is another example of such a distribution. My predictions on the most plausible immigration and emigration rates agree well with Cardinale et al. (2006) who did not observe any correlation between immigration rates and aphid density.

Fryxell et al. (2004) studied patterns of dispersal for Thomson’s gazelles (Gazella thomsoni thomsoni Günter) on the Serengeti Plains of East Africa. They assumed that probability of emigration depends on the local energy gain relative to the expected rate of daily energy gain averaged over the landscape. Such a rule implicitly assumes that animals have a global knowledge of their environment. They investigated several modes of immigration rates and they found that gazelle movements were best predicted by the model where probability of immigration into neighboring sites was determined by relative rates of energy intake. The discrepancy between their predictions and predictions for lady beetles can be caused by several factors. First, both models differ in how emigration rates depend on patch quality. While my models assume that emigration depends only on the quality of the current patch, Fryxell et al. (2004) assume emigration rates to be dependent on both the quality of the local patch as well as the average quality of all patches. Second, the discrepancies can be due to different rules for herbivore vs. predator dispersal.

An important assumption made in this article is that the observed distribution corresponds to a stable equilibrium pattern of lady beetle dispersion among aphid patches. This requires that patch quality given by aphid numbers is at least temporarily fixed. Honěk’s data used in this article come from a largely uniform habitat in which aphid and lady beetle populations had been building for a few weeks so that a temporary equilibrium in beetle distribution may well have been reached. Aphid local populations are often ephemeral (boom and bust) so on a longer time scale the assumption on fixed patch quality is not justified and aphid population dynamics must be taken into account.

ACKNOWLEDGMENTS. I wish to thank A. Honěk for sending me the original data on lady beetles distribution, I. Hodek who greatly helped me in thinking on this topic, E.W. Evans and an unknown reviewer for their suggestions that greatly improved this article. This work was supported by GA AV (I/AA100070601). Institute of Entomology is funded by AS CR (Z500750508).

REFERENCES


Houston A.L., McNamara J.M. & Milinski M. 1995: The distribution of animals between resources – a compromise between


Jackson A.L., Ranta E., Lundberg P., Kaitala V. & Ruxton G.D. 2004: Consumer-resource matching in a food chain when both predators and prey are free to move. *Oikos** **106**: 445–450.


Received September 18, 2007; revised and accepted November 26, 2007