

Individuals on the landscape: behavior can mitigate landscape differences among habitats

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We present a case study of the rose hip fly, *Rhagoletis basiola*, to demonstrate how one can connect landscape to population and evolutionary dynamics through the responses of individuals. Survey data from six different isolated rose habitats (*Rosa* sp.) near Vancouver, Canada were analyzed to determine the spatial distribution of rose hips within and among bushes. Rose hips were clumped at all sites; there was statistically significant variation in degree of clumping among sites. However, analyses using dynamic life history theory suggest that much of this variation may be mitigated by oviposition and movement response of individual flies to fruit distribution: sites that differ structurally may not differ evolutionarily. With this in mind, we provide five different indices that could be used to evaluate fly performance on different landscapes: 1) the probability that a cell r units away contains resource, given that the current cell contains resource, 2) the probability that a cell r units away contains resource, given that the current cell is devoid of resource, 3) the optimal distance to move from a cell that harbors fruit, 4) the optimal distance to move from a cell that is devoid of fruit, and 5) the Expected Reproductive Success of a fly in a particular habitat. Those indices provide the link between landscape and individual behavior and suggest another way of addressing habitat conservation issues.

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It is generally agreed that landscape is essential to the population dynamics, evolutionary dynamics, and conservation biology of organisms. Habitat is the template on which ecological and evolutionary interactions are played out (Southwood 1988).

There is less agreement, however, about the importance of the individual response to environmental structure (cf. With and Crist 1995, Lima and Zollner 1996). The historical reasons for ignoring individual responses are many. First, until recently we lacked conceptual and computational methods for predicting the responses of individuals to the habitat. Second, although variation is the core of biology, typological thinking still dominates much of biology (Mayr 1988). If one thinks typologically, then organismal responses to the

environment are fixed and stereotypical, which makes them of possible consequence but little interest. Third, individual variation in response is often viewed as “noise”. That is, one may admit variation in individual responses, but does not attribute biological import to these variations.

It is our contention that individual behaviors do matter and we will show how individual responses may be critical to persistence of populations on the landscape and appropriate conservation decisions. To do this, we connect the landscape to population and evolutionary dynamics through the responses of individuals. Our case study uses the rose hip fly *Rhagoletis basiola* (Tephritidae), which attacks the hips (fruits) of wild roses. After describing the study system, we show how

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Table 1. Descriptive statistics (min, max) for 6 different *Rosa* sp. sites near Vancouver, Canada.

Site	No. bushes sampled	Bush height (m)	Bush width (m)	Bush depth (m)	Gap width (m)	Distance to next nearest site (km)
AG	16	0.5, 2	1, 8	1, 2	1, 10	0.5
QB	5	1, 2	1, 11	1, 7	1, 6	0.5
PA	15	1, 3	1, 18	1, 4	1, 20	0.5
NB	14	2, 3	1, 22	1, 2	1, 23	>1.0
CR	5	1, 2	2, 10	1, 4	1, 10	>2.0
JDF	12	1, 1.5	0.5, 12	0.5, 1.5	1, 12	>3.0

to identify the spatial structure of landscapes, in terms of the location of resources, conditioned on the resources at the current spatial location. We then show how individual behavior can link the landscape with evolutionary dynamics; it is this link that provides critical information when one faces difficult conservation decisions (Curio 1996).

The study system

Rhagoletis basiola is a univoltine, monophagous tephritid fly that infests the fruit of rose bushes (*Rosa* spp.). Females visually search for rose hips (Roitberg 1985) by hopping from leaf to leaf. Upon finding such fruit, females lay single eggs in rose hips and subsequently mark those fruits with oviposition pheromones to indicate the presence of viable eggs (Averill and Prokopy 1981, Roitberg and Mangel 1989). *R. basiola* females frequently avoid laying second eggs in egg-infested (marked) fruit because larval competition can entail fitness costs (van Alphen and Visser 1990). Feeding maggots cause necrosis in the rose hip but little or no damage is done to the seeds. After about three weeks in the fruit, the mature maggots drop to the ground and burrow into the soil, where they pupate and overwinter. Most individuals emerge the following year. Female adults experience daily survivorship approximating 0.95, determined by several direct and indirect measures (Roitberg 1989, Mangel and Roitberg unpubl.). The main contributors to adult mortality are spiders (Mather and Roitberg 1987, Mangel and Roitberg unpubl.). Flies may be caught in webs while moving through bushes or may be preyed upon by jumping spiders or crab spiders when visiting leaves or fruit. Aside from larval competition, a single species of parasitoid, *Halticoptera rosae* (Hymenoptera: Pteromalidae), is the primary mortality agent of immature flies. The wasp uses the marking pheromone of the fly to locate eggs and young larvae (Roitberg and Lalonde 1991).

Female *R. basiola* flies search within and among rose bushes for fruit. Mark-release experiments (Roitberg and Mangel unpubl.), observations and work conducted on a congener, *R. pomonella* (Roitberg et al.

1982, Roitberg and Prokopy 1983, 1984) strongly suggests that the tendency for an individual to move between bushes is a function of fruit density and quality as well as the distance between those bushes.

R. basiola is monophagous to the genus *Rosa*. Our work deals primarily with attacks on *Rosa nutkana* though some of our study sites include bushes that appear to be hybrids of *R. nutkana* and *R. pisocarpa* in which multiple fruit are sometimes borne at branch tips. Mature *R. nutkana* bushes vary in size from 1 to 3 m in height and spread asexually to form continuous stands several m in width (up to about 20 m at our study sites). *Rosa nutkana* is generally found at open habitats such as roadsides, clearings and meadows (Pojar and MacKinnon 1994).

Site descriptions

We investigate the relationship between rose hip distribution within and among 6 different isolated sites near Vancouver, BC or Vancouver Island and the relative fitness that (fly) behavioral variants obtain at these sites. Table 1 provides details on site-specific parameters regarding *Rosa* sp. architecture and availability. Below, we provide a general description of the 6 sites.

Agassiz (AG) – The *Rosa* sp. habitat is situated ca 100 km east of Vancouver, Canada. The habitat measures approximately 200 × 4 m and is defined by a drainage ditch that borders a fence adjacent to an alfalfa field. Bushes grow on the slopes of the ditch. *Rosa* is by far the dominant plant in the habitat, the next most common being snowberry, *Symphoricarpos albus*. We evaluated all of the bushes in this habitat.

Qualicum Beach (QB) – The *Rosa* habitat is situated on the east coast of Vancouver Island, ca 55 km north of Nanaimo. It forms part of an ocean side national wildlife refuge (Canadian Wildlife Service) for waterfowl. The habitat is found within a large (ca 0.5 × 0.5 km) meadow. *Rosa* is the dominant plant with mixed grass making up the bulk of the vegetation in the inter-*Rosa* spaces. Snowberry is also common at the site. We studied only those bushes in the open grass meadow.

Parksville (PA) – The *Rosa* habitat is situated on the east coast of Vancouver Island, ca 50 km north of Nanaimo. It forms part of an ocean side nature reserve. There are three *Rosa* habitats at the site: (1) *Rosa* bushes line a 150-m dirt trail that is adjacent to the Englishman River, (2) *Rosa* bushes are scattered within a grassy meadow adjacent to the Englishman River but on the opposite side of the 20-m tidal river from Habitat 1 and (3) *Rosa* bushes form a dense (100 × 100 m) mat within a grassy meadow. Habitat 3 is separated from Habitat 1 by 150 m of grassy meadow. We measured only those bushes in Habitat 1. Here, *Rosa* is the co-dominant species, along with broom (*Cytisus scoparius*) and blackberry (*Rubus ursinus*).

Nanose Bay (NB) – The *Rosa* habitat is situated on the east coast of Vancouver Island, ca 45 km north of Nanaimo. It forms part of a national wildlife refuge (Canadian Wildlife Service). The habitat measures approximately 500 × 6 m and is defined by a drainage ditch that borders a fence adjacent to a field of mixed grass. Bushes grow on the slopes of the ditch. *Rosa* is by far the dominant plant in the habitat, the next most common being blackberry and broom. We measured all of the bushes at the site.

Crofton (CR) – The *Rosa* habitat is situated on the east coast of Vancouver Island, ca 50 km south of Nanaimo. It is situated next to an unmanaged gravel pit. The site consists of two habitats that are separated by ca 50 m of vegetation-free gravel. Habitat 1 is a small 20 × 20 m grassy meadow that harbors a small cluster of 3 large and 2 small bushes. Habitat 2 is a considerably larger (ca 100 × 100 m) gravel, sparse-grass meadow wherein *Rosa* bushes are scattered. We studied only those bushes at Habitat 1. There, *Rosa* is co-dominant with mixed grasses and blackberry.

Juan de Fuca (JDF) – The *Rosa* habitat is situated on the south-west coast of Vancouver Island, ca 100 km east of Victoria. It is part of an unmanaged ocean-side (ca 100 × 25 m) picnic site that is situated on a large rocky outcropping that overlooks the Pacific Ocean. Here, plants are scattered across open rocks and along the edge of a forest trail. Plants at the former site, the only place where we took measurements, are co-dominant with salal (*Gaultheria shallon*).

Methods

Structure functions describe the landscape

We begin by considering an organism foraging (in this case for reproductive sites) in a landscape with spatial structure. For simplicity, we imagine the world divided into discrete cells (for the rose hips, we used 5-cm cells). Each cell either contains resource or does not. The structure of the landscape is summarized by conditional information: given that the individual is at a site that

contains resource or is devoid of resource, we specify the probability (called the structure function) that a site some distance away contains resource (Mangel 1994, Mangel and Adler 1994)

$$\begin{aligned} p(r | 1) &= \text{Prob} \{ \text{a cell } r \text{ units away contains resource,} \\ &\quad \text{given that the current cell contains} \\ &\quad \text{resource} \} \\ p(r | 0) &= \text{Prob} \{ \text{a cell } r \text{ units away contains resource,} \\ &\quad \text{given that the current cell is devoid of} \\ &\quad \text{resource} \} \end{aligned} \quad (1)$$

If \bar{p} is the average density of resources in the environment, then the two structure functions $p(r | 1)$ and $p(r | 0)$ are connected by the relationship

$$p(r | 1) + (1 - \bar{p})p(r | 0) = \bar{p} \quad (2)$$

That is, on average when one moves a distance r from a cell, the chance of encountering resources should be \bar{p} . The chance the cell being vacated contains resources is \bar{p} and the chance that the cell being vacated is devoid of resources is $1 - \bar{p}$; hence eq. 2, which shows one needs to determine only two of the three quantities \bar{p} , $p(r | 0)$ and $p(r | 1)$. The average density of resources is found by dividing the canopy of the bush or tree into cells and estimating \bar{p} as the fraction of cells that contain resource.

To determine $p(r | 1)$, one proceeds as follows. Randomly select a cell that contains resources. Allow a number of rays to emanate from each cell containing resource, with directions randomly chosen. At unit distances (measured in the size of the cell), note if the cell a distance r from the target cell contains resources or not. We summarize this information by a variable $I_{kj}(r)$ which is 1 if the cell r units away on the k th ray from cell j containing resources contains resource and which is 0 otherwise. If a total of K rays are sampled from cell j , then an estimate of $p(r | 1)$ based on cell j is

$$p_j(r | 1) = \frac{1}{K} \sum_{k=1}^K I_{kj}(r) \quad (3)$$

If J cells with resource are used as starting points, then the estimate of $p(r | 1)$ is

$$p(r | 1) = \frac{1}{J} \sum_{j=1}^J p_j(r | 1) \quad (4)$$

We selected up to 20 bushes at each rose habitat. At each bush, we randomly chose a single cluster of fruit and then recorded the presence of fruit at 5-cm distances along 5 randomly chosen rays at angles of multiples of 45°. In addition, we measured the size of each bush as well as the distance or gap size between bushes (Table 1). Together, these data provide a measure of the conditional probability of fruit encounter $p(r | 1)$, averaged over the entire habitat. For example,

habitats with very small bushes and large gap sizes would give very low probability of host encounter following moves of moderate distance in that such moves would generally lead to flies finding themselves between bushes.

Results

Rose bushes differ, statistically, in structure

The six $p(r|1)$ functions split into 2 groups (Fig. 1a). Comparison of pairs of structure functions by a Kolmogorov-Smirnov test (with a sequential Bonferroni correction) demonstrates nearly identical, shallow trajectories of NB, CR and PA that are statistically indistinguishable while two other sites (AG, QB) have much steeper ($p < 0.001$) trajectories indicating a more clumped distribution of fruit than for the former group. The AG and QB sites are indistinguishable from one another. The JDF site appears to be intermediate between the two groups (p ranges from 0.15 to 0.5).

The six $p(r|0)$ functions split into 4 groups (Fig. 1b). NB and PA are statistically indistinguishable ($p > 0.5$); JDF and CR are statistically indistinguishable ($p > 0.15$); QB and AG are distinguishable even though they traverse a similar section of the plot space (Fig. 1b). Each of the 4 groups is significantly different from

one another ($p < 0.001$). Thus, there are statistically significant differences among the 4 habitat groups in the probability with which flies encounter fruits upon leaving a point at which no fruit is found although at all sites the $p(r|1)$ functions suggest that fruit are clumped, but to different degrees.

Notice that the $p(r|1)$ and $p(r|0)$ functions produce nearly inverse curves of one another. However, since they express probabilities that are dependent upon the state of the current cell (empty or occupied), and resources may be clumped to varying degrees, those functions are not mirror images. For example one can solve Eq. 2 to relate $p(r|0)$ to $p(r|1)$ as $p(r|0) = \bar{p}(1 - p(r|1))/(1 - \bar{p})$.

The rose hip sites may not be evolutionarily different: an appraisal based on dynamic life history theory

Given that fruits are clumped at all sites and in particular at QB, JDF and AG, there could be significant fitness costs to flies that exploit resources in a suboptimal manner. To evaluate the magnitude of these potential costs, we used dynamic life history models (Mangel and Clark 1988, Mangel and Ludwig 1992) to calculate the lifetime reproductive fitness of flies that move various distances from positions with and without resources (Mangel 1994). To do this, we characterized a behavioral strategy by the distance k_0 the fly moves from a position or cell devoid of hosts, the distance k_1 it moves from a position containing hosts and the clutch c that it lays when it encounters a cluster of fruit:

$F_0(t; k_0, k_1, c)$ = expected reproductive success from time t onwards for a fly currently at a cell devoid of hosts and following $\{k_0, k_1, c\}$

$F_1(t; k_0, k_1, c)$ = expected reproductive success from time t onwards for a fly currently at a cell containing hosts and following $\{k_0, k_1, c\}$ (5)

Because fitness in one period is linked to that in the next, we iteratively calculate lifetime reproductive success for flies at fruit-devoid and fruit-occupied cells. To do this, we must specify the search speed v , the mortality m during search, the mortality m_o during oviposition and the increment in lifetime reproductive success $R(c)$ from a clutch of size c . Then the two fitness functions are related by (Mangel 1994):

$$F_0(t; k_0, k_1, c) = (1 - m)^{k_0/v} \times [p(k_0|0)F_1(t + k_0/v; k_0, k_1, c) + (1 - p(k_0|0))F_0(t + k_0/v; k_0, k_1, c)] \quad (6)$$

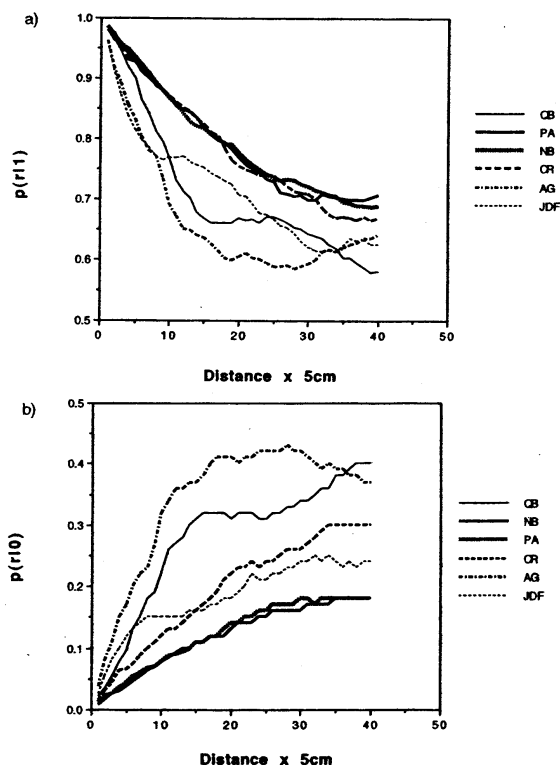


Fig. 1. The structure functions a) $p(r|1)$ and b) $p(r|0)$ at the different rose hip sites.

Table 2. Optimal movement distances, clutch sizes and lifetime reproductive success for rose hip flies in 6 different habitats as determined by landscape-based state variable models.

Param.	AG	QB	Site PA	NB	CR	JDF
k_0^*	2	11	1	3	4	3
k_1^*	1	1	1	1	1	1
c^*	3	3	3	3	3	3
ERS	10.0	10.0	7.6	7.4	9.5	8.2

and

$$F_1(t; k_0, k_1, c) = R(c) + (1 - m_o)(1 - m)^{k_1/v} \\ \times [p(k_1 | 1)F_1(t + k_1/v; k_0, k_1, c) \\ + (1 - p(k_1 | 1))F_0(t + k_1/v; k_0, k_1, c)] \quad (7)$$

We estimate $m = 0.01$ and $m_o = 0.001$ from laboratory (Roitberg 1989) and field (Mangel and Roitberg unpubl.) studies, set $v = 1$ cell/min and

$$R(c) = 1.0c(\max 0, 1 - (c/5)^3) \quad (8)$$

The parabolic shape from eq. 8 is determined by the strong within-host larval competition expressed by *R. basiola* and other solitary, temperate-zone tephritids (Averill and Prokopy 1987) and a fixed fruit cluster size of 3 (non-varying to reduce complexity).

We disregard egg complement as a state variable to reduce the complexity of the problem. In addition, we assume that flies at a given site behave as if the structure function at that site is known (for details on how to implement information state in these models see Mangel and Roitberg 1989). We calculated the long-time expected reproductive success (ERS) from eqs 6 and 7 by setting $F_1(t; k_0, k_1, c) = F_1(t + k_1/v; k_0, k_1, c) = F_1(k_0, k_1, c)$, doing the same for $F_0(k_0, k_1, c)$ and solving the resulting algebraic equations. Finally, we averaged the stationary solutions over the starting points (cells either with or without hosts).

The optimal clutch size ($c^* = 3$) and movement rule from a cell containing hosts, $k_1^* = 1$, is the same for all sites (Table 2). In contrast k_0^* varies from 1 to 11 at PA and QB, respectively. These differences can be explained by examining the $p(r | 0)$ functions in Fig. 1b. For QB, the probability of host encounter rises rapidly at nearly twice the rate than it does for PA. This offsets the cost of moving in the former but not in the latter habitats. Further, lifetime reproductive success varies from 7.4 (NB) to 10.0 (AG and QB). Thus, with our choice of $R(c)$, all populations are growing (presumably producing emigrants).

To evaluate the potential fitness consequences of suboptimal movements, we calculated the lifetime

fitness for $k_0^* + 1, k_0^* + 2, k_0^* + 3, k_0^* - 1, k_0^* - 2, k_0^* - 3$ and $k_1^* + 1, k_1^* + 2, k_1^* + 3$. Of course, in some cases (e.g. $k_0^* = 1$) it was not possible to explore the full range of values because negative distances would arise. Such calculations generate fitness surfaces (Mangel and Ludwig 1992) that characterize the sites (Fig. 2).

With the exception of QB, all of the fitness surfaces are asymmetrical (Fig. 2a), so that flies that consistently move greater than optimal distances from empty cells receive greater decrements to fitness than flies that consistently move equally lower-than-optimal distances. Furthermore, the k_0 -fitness surfaces vary among the sites, although QB, NB and AG all display rather flat surfaces; at the extreme, for movements of 15 cm more-than-optimal distance, individuals experience, at most, a 5% reduction in lifetime reproductive success. The functions at the other three sites are steeper but, even so, are relatively flat.

Since $k_1^* = 1$, the k_1 -fitness surfaces (Fig. 2b) only involve move distances greater than optimal. In this case, the fitness surfaces at all six sites are steep such that $k_1^* + 3$ leads to greatly reduced lifetime fitness values (ca 30% of optimal). Thus, we predict strong selection for flies at all sites to exhibit classic "area

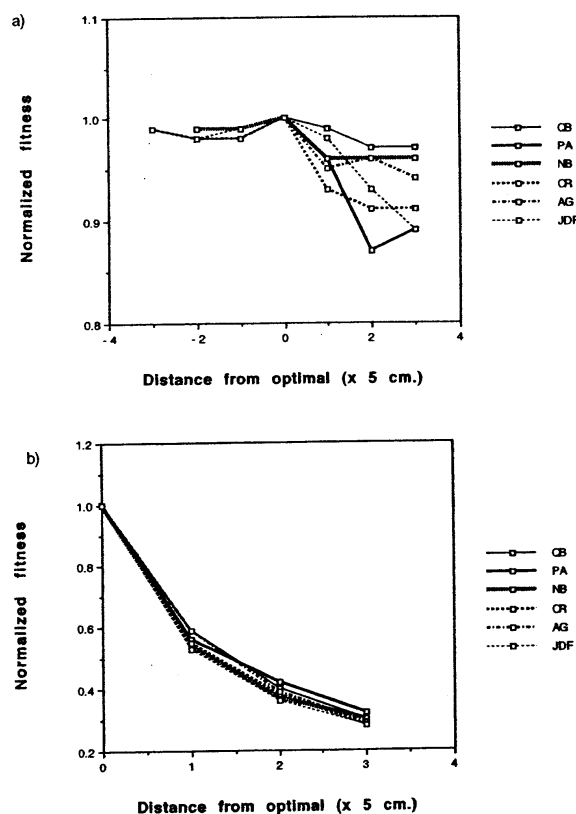


Fig. 2. Normalized fitness surfaces at the rose hip sites. a) k_0 -fitness surfaces are generally symmetrical. b) Since $k_1^* = 1$ at all sites, we can only study deviations that are larger than optimal.

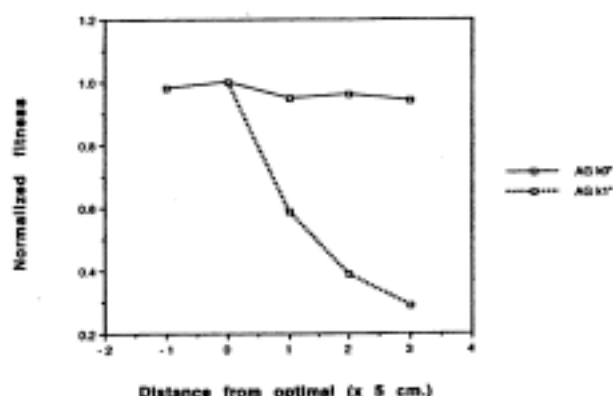


Fig. 3. The normalized lifetime reproductive success surface at Aggasiz suggests weak selection on movement from empty sites but strong selection on movement from full sites.

restricted search" (Bell 1991, Benhamou 1992). Finally, the normalized fitness surfaces at all six sites are nearly identical with maximum deviations between the normalized curves of less than 8%.

Comparing the k_1 - and k_0 -fitness surfaces provides insights into the evolutionary forces that could shape foraging behavior of rose hip flies (see Carriere and Roitberg (1996) for methodology on incorporating a genetic component). For example, Fig. 3 shows the significant difference in degree of trajectory for the two surfaces at AG. Clearly, deviations from k_1^* are likely to be under strong selection relative to k_0^* . We calculated the intensity of selection on k_0 and k_1 movement traits by the methods of quantitative genetics (Falconer 1989). We assume that the tendency-to-move traits are uncorrelated with values that are normally distributed (mean = k_0^* or k_1^* and standard deviation = 1.0). Since by definition, k values can only be positive and $k_1^* = 1$ at all sites, we could only evaluate directional selection on suboptimal move-tendencies where k_1 exceeded 1. Thus we can only calculate directional selection against excessive mobility (Endler 1986) for both k_0 - and k_1 -fitness surfaces, though we acknowledge that stabilizing selection is likely to be an important determinant of k_0 .

Selection differentials for k_0 at all sites are very low, ranging from -0.004 at PA to -0.02 at CR. By contrast selection differentials for k_1 range from -0.12 at QB to -0.13 at NB; these are substantial given that they were determined with the mode of k_1 set at k_1^* . We interpret these results as follows: since $k_1^* = 1$ at all sites and since the k_1 -fitness functions are steep, we would expect to see similar success-motivated search patterns from flies at all sites even if such sites were isolated and their populations experienced little gene flow from other populations. This appears to be the case (Roitberg unpubl.). By contrast, the relatively flat fitness surface (low selection differentials) for the k_0 functions at all sites should permit variation in that trait to persist both within and among sites. For example, with a heritability of 0.50, we predict a 0.1% change in the

mean k_0 phenotype in the PA population in a single generation, even with the restrictive assumptions that we posited (Endler 1986). Thus, even though there is considerable statistically distinguishable variation in resource structure among the different sites, this variation is likely to have little impact on oviposition-related foraging behaviors.

Our interpretation of localized search patterns may be considered from a landscape perspective, i.e., it transcends several hierarchical levels of scale. Structure functions describe the relationship between patchiness at the very local (cell) and the more global (habitat) level. In other words, it is explicit in our theory that oviposition decisions at the cell level depend upon within- and among-bush parameters. In addition, we also know from mark-recapture experiments (Roitberg and Mangel unpubl.) that there is little movement of flies between sites that are separated by 1 km or more. Thus, most of the dynamics are generated by within-habitat events at each of the sites that we studied.

Conservation on the landscape and the importance of individuals

The structure function, which is based on the implicit assumption that there is pattern – albeit only probabilistic pattern – in the wildness of biological diversity, allows one to connect life history and the landscape in which the organism finds itself. It provides a means to put the organism back into conservation biology in a meaningful way.

Although landscapes may differ in their structure, behavior of the individual may mitigate these differences, so that from the perspective of the evolutionary ecology of organisms, the landscapes are similar. Thus, it may be critical to not only characterize the landscape, but to be able to characterize the response of individuals to the landscape. Our work shows that if behaviors are not particularly plastic – so that each population has an evolved response that is specific to its habitat, then there is a method of justifying the protection of the habitat. Too often, conservation biology has ignored individual variation.

On the other hand, one of the great challenges of conservation arises because not everything can be conserved; we often face the agony of choice. In the case study here, the problem might be to determine a priority ranking for protecting the rose hip fly habitats. The first step might be identifying which habitats are "similar"; for this we have at least five potential mechanisms for comparing habitats: $p(r|1)$, $p(r|0)$, k_1^* , k_0^* , and Expected Reproductive Success. Since, in this case, k_1^* is the same at all sites, it provides no information. Letting $\{ \}$ denote sites that are functionally equivalent, based on $p(r|1)$, we group the sites as

{NB, CR, PA}, {JDF}, {AG, QB}

while based on $p(r|0)$ we group them as

{NB, PA}, {JDF, CR}, {QB}, {AB}.

Thus, based on structure, NB and PA are equivalent sites. Based on k_0 , we group the sites as

{PA}, {AG}, {JDF, NB}, {CR}, {QB}.

Finally, based on Expected Reproductive Success, we group the sites as

{AG, QB}, {PA, NB}, {CR}, {JDF}.

Thus, our work gives support for protection of most of the sites and a mechanism for choosing which might be lost, if one has to be lost.

Lima and Zollner (1996) argue that behavioral and landscape ecology are poised for a productive union and that what has separated them is the very different spatial scales at which landscape and behavioral ecologists work. Our work shows how this gap may be bridged and is one of the first contributions towards the behavioral ecology of landscapes.

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