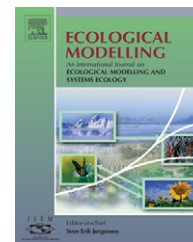


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## Short communication

# Accounting for possible detectable distances in a comparison of dispersal: Apollo dispersal in different habitats

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### ABSTRACT

Estimates of dispersal distances, when studied using mark-release-recapture techniques, are affected by many extrinsic factors such as study area size, local population density, and landscape configuration. We show that a comparison of observed dispersal distances between groups (e.g. sexes, populations, study periods) may lead to erroneous conclusions when groups differ in their distribution of possible detectable distances (the distribution of all distances in the system weighted by the number of marked individuals that have the possibility to move those distances). We show how this distribution can be used to: (1) test whether the scale of the study area is adequate for a description of mean dispersal; (2) express dispersal as a fraction of the number observed over the number of possible detectable movements for each distance. Dispersal scaled in this fashion can be compared between groups using standard statistical techniques. For illustration, we analyse five mark-release-recapture studies on the Apollo butterfly *Parnassius apollo* from two populations. Correcting for possible detectable distances shows that dispersal in an archipelago population is lower than in a coastal population, possibly due to harsher habitat between the patches in the former population.

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## 1. Introduction

Dispersal is one of the cornerstones of population biology (Clobert et al., 2001; Bullock et al., 2002). A species' capacity for dispersal is typically quantified on the basis of observed distances of marked individuals that are recaptured at some distance from their site of release (Mark-release-recapture MRR, e.g. Bennetts et al., 2001). However, it remains currently unclear to what extent dispersal tendencies across species and across different populations of the same species can be compared using this technique. Here,

we recognise that each observed distribution of dispersal is partly a function of the organism's dispersal tendency, but is also influenced by a number of extrinsic factors such as landscape configuration and by the size of the study area. We present a general technique to correct for such extrinsic factors, and which can be used to compare the tendency to disperse between groups using standard statistical techniques. We employ our approach in a comparison of dispersal between two populations of the Apollo butterfly *Parnassius apollo* that differ in their landscape structure.

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2. Materials and methods

The recapture of a marked individual in another site than where it was released is recorded as a dispersal event of a certain distance given by the distance between the sites. All such events together create a distribution of observed dispersal distances. We here refer to the site of capture as a patch, because we envision individuals that occur on a number of discrete patches that together form a network (landscape). In more homogenous or non-exhaustively sampled landscapes, the site of capture could also be defined by its coordinates on a grid.

For every patch  $i$  and  $j$  ( $i \neq j$ ) in a system of patches, we observe  $N_{ij}$  movements of distance  $d_{ij}$  (either from patch  $i$  to patch  $j$ , or vice versa). The maximum possible number of individuals that can move  $d_{ij}$  is given by  $\Sigma_{ij}$ , the sum of marked and released individuals on patches  $i$  and  $j$ . A given interpatch distance is only possible to detect if there were marked individuals released on either of these patches ( $\Sigma_{ij} > 0$ ), and becomes more likely to be detected when relatively more individuals are released. This distribution, which we here term possible detectable distances, is the distribution of all interpatch distances weighted by  $\Sigma_{ij}$  and forms a probability function for detecting a given distance.

For the example landscape of Fig. 1A, we could have marked two groups (e.g. males and females, two different study periods, two different species) and recorded the same observed distribution of distances moved (Table 1). The two groups differ in the distribution of possible detectable distances (Table 1). We can correct for this underlying difference by calculating the fraction of observed over ‘maximally possible’ dispersal ( $N_{ij}/\Sigma_{ij}$ ) for each distance  $d_{ij}$  (Table 1). This quantity therefore describes the probability for dispersing a certain distance that is independent of the landscape configuration and the number of marked individuals. By directly comparing the observed distribution (Table 1), we would conclude that in both groups 58% (14/24) of individuals dispersed the same average distance. We can formally test the statistical significance of the dispersal corrected for the possible detectable distances by using logistic regression (because the response is a ratio between zero and one). In this example, we find significant differences between the groups (Fig. 1B), where group two is more prone to make shorter dispersal movements than group one.

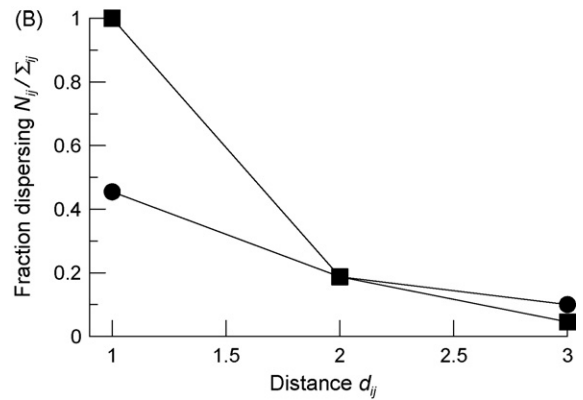
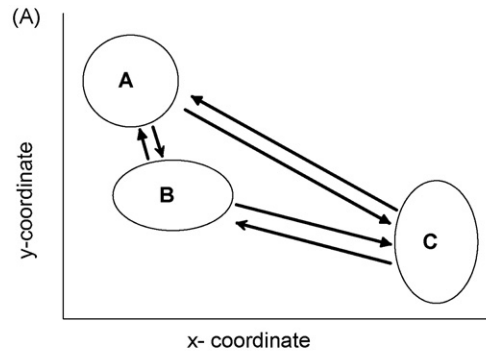


Fig. 1 – (A) Schematic illustration of a landscape of three patches. Every possible movement is illustrated by a vector, where the length is related to the distance moved. (B) Plot of the fraction of marked individuals on patches  $i$  and  $j$  that dispersed the interpatch distance  $d_{ij}$ , based on the data in Table 1. Group one is plotted with a filled circle and group two with a filled square. The fraction is the number of observed movements  $N_{ij}$  between patch  $i$  and  $j$  for a given distance class  $d_{ij}$ , divided by  $\Sigma_{ij}$ , the total number of individuals marked on these patches. Note that the fractions are calculated within each distance class  $d_{ij}$  and therefore do not sum to one across distance classes. Although the groups have the same observed distances moved, the dispersal tendency of group two is clearly different when correcting for the possible detectable distances—logistic regression, distance  $\chi^2_1 = 5.6, P = 0.02$ ; Group  $\chi^2_1 = 8.3, P = 0.004$ ; interaction  $\chi^2_1 = 5.6, P = 0.03$ .

Table 1 – Number of observed movements (from patch  $i$  to target patch  $j$  and vice versa), with the number of individuals marked on patches illustrated in Fig. 1

Movement	Distance ( $d_{ij}$ )	Observed movements ( $N_{ij}$ )	Number marked on both patches ( $\Sigma_{ij}$ )	
			Group 1	Group 2
A-B/B-A	1	10	22	10
B-C/C-B	2	3	16	16
A-C/C-A	3	1	10	22

There were 14 recorded movements, two groups each of 24 marked individuals, that were released over the patches, but where the distribution of markings differed across patches: In group one, 8 individuals on patch A, 14 on B, and 2 on C; in group two, 8 on patch A, 2 on patch B and 14 on patch C. For each particular pair of patches, the two groups differ in the sum of individuals marked ( $\Sigma_{ij}$ ).

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