

# Relative importance of host plant patch geometry and habitat quality on the patterns of occupancy, extinction and density of the monophagous butterfly *Iolana iolas*

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**Abstract** Habitat fragmentation is a major cause of species rarity and decline because it increases local population extinctions and reduces recolonisation rates of remnant patches. Although two major patch characteristics (area and connectivity) have been used to predict distribution patterns in fragmented landscapes, other factors can affect the occurrence of a species as well as the probability of it becoming extinct. In this paper, we study the spatial structure and dynamics of the butterfly *Iolana iolas* in a 75-patch network of its host plant (*Colutea hispanica*) to determine the relative importance of patch area, connectivity and habitat quality characteristics on occupancy, extinction and density over the period 2003–2006. Occupancy in 2003, incidence (proportion of years occupied) and probability of extinction were mostly affected by patch area. Smaller patches were less likely to be occupied because they had a higher probability of extinction, partly due to environmental stochasticity. The density of *I. iolas* was negatively related to patch area in all study years. Only in 2004 was the density of *I. iolas* positively influenced by fruit production per plant. Our results suggest that for *I. iolas*, and probably for other specialist butterflies with clearly delimited resource requirements, metapopulation dynamics can be satisfactorily predicted using only geometric variables because most habitat characteristics are subsumed in patch area. However, this hypothesis should

be subject to further testing under diverse environmental conditions to evaluate the extent of its generalisation.

**Keywords** *Iolana iolas* · Metapopulation · Occupancy · Patch quality

## Introduction

Identification of the factors that affect the spatial and temporal dynamics of populations of species living in fragmented landscapes in one of the major goals of conservation biology. The most popular approach is metapopulation theory, which has been successfully used to describe the patterns of occupancy, extinction and colonisation of a wide range of species (McCullough 1996; Hanski and Gilpin 1997; Hanski and Gaggiotti 2004). Metapopulation studies have often shown that patch occupancy patterns can be satisfactorily predicted on the basis of two geometric variables, patch area (as surrogate of population size) and isolation (or inversely, connectivity) (e.g. Kindvall and Ahlén 1992; Thomas and Harrison 1992; Thomas et al. 1992; Bergman and Landin 2001; James et al. 2003; Menéndez and Thomas 2006; Öckinger 2006). These two variables are related to two major processes driving local and regional dynamics through metapopulation processes: the increase of stochastic extinctions with decreasing patch size, and the decrease of (re)colonization probability of empty patches with increasing isolation (Hanski 1994a). Based on these processes, theoretical models predict a smaller probability of occupancy for small and isolated patches relative to large and well-connected ones.

Nevertheless, habitat characteristics other than size and connectivity, such as habitat quality, have been proven to

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be important determinants of species occurrence patterns (Sjögren-Gulve and Ray 1996; Fleishman et al. 2002). In the case of Lepidoptera, habitat quality has been quantified in terms of adult and larval food resources, vegetation structure, topography and microclimate (e.g. Fleishman et al. 2002; James et al. 2003; Krauss et al. 2004, 2005; Binzenhöfer et al. 2005). As a result, most current metapopulation studies also include effects of habitat quality, although its importance relative to that of area and isolation remains controversial (Dennis and Eales 1997, 1999; Moilanen and Hanski 1998; Thomas et al. 2001; Fleishman et al. 2002; Dennis et al. 2003, 2006).

While most metapopulation research have focused on occupancy patterns, less attention has been paid to the variation in density between occupied patches (Förare and Solbreck 1997; Krauss et al. 2004, 2005; Nowicki et al. 2007) and the temporal turnover of patches (Kindvall and Ahlén 1992; Förare and Solbreck 1997; Fleishman et al. 2002; González-Megías et al. 2005). Because patch areas are used as surrogates of population sizes in metapopulation studies, the relationship of density with patch area and additional quality variables is crucial an understanding of the patterns of occupancy and turnover in habitat patches as well as the long-term dynamics of fragmented systems. Within a network of habitat patches, increasing or decreasing density with area aggregates individuals into large or small patches, respectively, changing the relative importance of different patch sizes on metapopulation dynamics (Connor et al. 2000; Matter 2000). Further, because spatial patterns change in time, it is necessary to carry out relatively long-term studies to evaluate the temporal variations in occupancy, extinction, colonisation and density patterns as well as the intensity of synchronous dynamics of local populations, since the expected persistence time of a metapopulation decreases as the spatial synchrony among local population increases (Harrison and Quinn 1989; Liebhold et al. 2004).

All of the issues mentioned above have been individually addressed in empirical and theoretical studies. However, integrative approaches including spatial as well as temporal patterns of patch occupancy and abundance have been rarely conducted in empirical metapopulation studies (e.g. Förare and Solbreck 1997; Hanski 1999), despite the fact that they are crucial to understanding the dynamics of fragmented systems.

We have simultaneously studied the spatial and temporal patterns of occurrence and abundance of the endangered specialist butterfly *Iolana iolas* (Lycaenidae) in a 75-patch network in central Spain during four consecutive years. This species is particularly appropriate as a model system to address these issues because: (1) *I. iolas* has a highly fragmented distribution following the distribution on its only host plant in the area *Colutea hispanica*

(Rabasa et al. 2005); (2) the study system has been proven to show metapopulation processes, with moderate emigration rates among discrete local populations (Rabasa et al. 2007); (3) there is previous evidence that *I. iolas* density as well as *C. hispanica* flower and fruit production (adult and larval resources, respectively) are highly variable among years (Rabasa et al. 2005, unpublished). Specifically, the main issues of our study are: (1) to test the effects of habitat characteristics (topographical factors, microclimate, resource quantity) and standard geometric measures (area and connectivity) of patches on the occurrence, turnover and density of the butterfly *I. iolas*; (2) to determine the temporal variability in population density and resource quantity (fruit production) with the aim of detecting the level of synchrony between patches over a 4-year period.

## Methods

### The species

*Iolana iolas* (Lycaenidae) occurs with a patchy distribution throughout southern Europe and the Magreb (Tolman and Lewington 1997). This species is classified as “endangered” in the Iberian Lepidoptera Red Data Book (Viedma and Gómez-Bustillo 1985) and is included in the regional list of endangered flora and fauna of the Autonomous Community of Madrid as a “species sensitive to the alteration of its habitat” (Anonymous 1992; Munguira and Martín 1993). *Iolana iolas* is a single-brooded species, flying from late April to early July (Munguira 1989). It is a monophagous species whose adults and larvae feed on flower nectar and seeds respectively, of plants of the genus *Colutea*. Females lay eggs on the calyx of the developing fruit, and the caterpillars end their development by July (Munguira 1989; Munguira and Martín 1993; Rabasa et al. 2005). *Iolana iolas* overwinters as pupae from which adults emerge the next spring. Its host plant in the study area, *C. hispanica*, is a rare shrub that occurs in limestone and gypsum soils (Talavera and Arista 1998), and it is the only species of the genus in Madrid. It is almost a complete summer semideciduous perennial shrub, reaching 2–3 m in height and flowering between April and June. Because *C. hispanica* is a long-lived shrub and seedlings are rarely seen in the field, patches contained the same total number of host plants and thus patch area was kept constant from year to year.

### Study system

The study was conducted in a gypsum outcrop area located near Chinchón, approximately 45 km southeast of Madrid,

Central Spain (centred on 40°08'N, 3°28'W), for a 4-year period from 2003 to 2006 (Fig. 1). The study area is a fragmented landscape dominated by sparse perennial vegetation of *Stipa tenacissima* tussocks with some remnants of Mediterranean woodland consisting of *Quercus coccifera* and *Q. rotundifolia* and scattered populations of *C. hispanica*. This area is sharply bounded to the south by extensive olive groves and to the north by irrigated fields where *C. hispanica* does not occur. The climate is semi-arid Mesomediterranean with a mean annual temperature of 14.2°C and average annual rainfall of 438 mm (data from Arganda del Rey thermopluviometric station,  $n = 29$  years). Mean daily maximum and minimum temperatures are, respectively, 10.6 and 0.2°C in January, and 33.1 and 15.5°C in July. There is a pronounced summer drought from May to September.

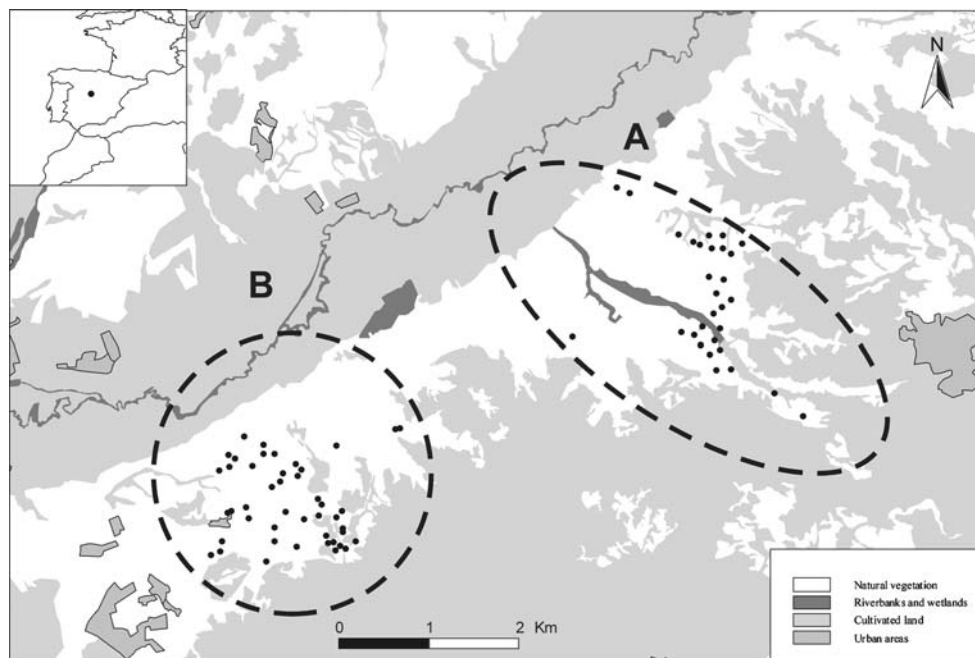
During January–April 2003, we mapped the distribution of *C. hispanica* in a 60-km<sup>2</sup> area using a GPS hand-held receiver (GPS model 12XL; Garmin Int, Olathe, KS) and 1:5000 maps. We found a total of 75 patches of *C. hispanica* subdivided in two subsystems that were more than 2 km apart, one consisting of 45 patches and other of 30 patches (Rabasa et al. 2005). *Colutea hispanica* has a highly clumped distribution pattern in Central Spain which allows patches in the field to be easily delineated (densities within patches are relatively high, averaging approx. 13 plants/100 m<sup>2</sup>). The criteria used to consider separate (distinct) patches were if their boundaries were separated by 40 m or more of terrain with no *C. hispanica* or, in a few cases, by a shorter distance if there was a distinct land cover change (e.g. cultivated land). This distance is

comparable to the boundaries between patches or populations in other butterfly metapopulation studies (e.g. Wilson et al. 2002). In a mark–release–recapture study carried out in a subsystem of 18 patches, Rabasa et al. (2007) found that butterflies moved a median distance of 29 m between successive recaptures and that approximately 42% of recaptured individuals of *I. iolas* transferred between patches defined in this way.

#### Patch occupancy and extinction

To determine the occupancy status of *I. iolas* on patches we walked standard butterfly transects (Pollard and Yates 1993) in all patches during the flight period in 2003, 2004, 2005 and 2006. In addition, we carried out extensive searches for *I. iolas* eggs in all patches during the same period and, for those patches in which no eggs were found, at the end of the flight period. Eggs are easily distinguishable on the basis of their external morphology (Munguira 1989). Fruits in each patch were carefully checked until an egg was found in a sample of up to 150 fruits, or all fruits if there were less than 150 eggs. We are confident that by using this method, consistent failure in finding both adults and eggs in a patch means a “true absence”. Patches were classified as “occupied” in a year when either adults or eggs were present. For each year we modelled occupancy as a binary variable (presence = 1, and absence = 0). We also calculated the incidence of *I. iolas* per patch during the 4-year period as the proportion of years with butterfly and/or egg occurrences. We recorded extinction in a patch as the occupancy status change

**Fig. 1** Map of the study system showing the location of the 75 study patches. Dashed lines indicate the two *Colutea hispanica* subsystems of 30 (a) and 45 (b) patches



from occupied to unoccupied in two successive years. Because the number of yearly extinctions was small for the analyses, we estimated an extinction rate per patch for all years pooled as a binary response of 0 if patches were occupied in all 4 years, and as 1 if at least one extinction event had occurred in one or more years. Although colonisation events were also recorded during the study period, no patch was permanently vacant during the whole period (see results below). This fact prevented us from making comparisons between the attributes of colonised versus non-colonised patches.

#### Population size and density

In 2003, 2004 and 2005, there was insufficient time to assess population sizes at peak of the flight period at all patches; in those cases, we walked transects at peak in a sample of 30 patches located in the western subsystem (Fig. 1). All patches were visited during the peak of the flight period in 2006.

We calculated a population index (PI) following Thomas (1983):

$$PI = 100 NA/L \quad (1)$$

where  $N$  is the butterfly count of each transect at the flight peak;  $A$  is the area of each patch in hectares;  $L$  is the length of transect in metres. We estimated population sizes (PS) of *I. iolas* in each year from transect counts at the flight peak using the following regression equation calculated in a previous study in which we compared daily population mark–release–capture estimates with PIs estimated from transect counts in the same day (Rabasa et al. 2007):

$$PS = 13.266 PI; \quad r^2 = 0.81, \quad N = 11, \quad P < 0.001 \quad (2)$$

Since about one third of individuals usually fly at the flight peak in butterflies (Bergman 2001; Välimäki and Itämies 2003), we estimated total population sizes by multiplying the population size estimate at the flight peak by 3. There were a variable number of small patches in which no individual was seen during transect counts but where there was evidence of *I. iolas* presence in that year based on egg occurrence. Excluding these “false zero” patches would imply estimating the relationship between density and area (and other variables) over a narrower range and a biased sample of butterfly densities and patch areas. Because this fact may potentially result in biased density–area relationships, we included patches with eggs but no butterfly records in our analyses (Connor et al. 2000; Brotons et al. 2003). In those cases, we assigned a minimum population size value of one individual, which is in line with the minimum value of population sizes estimated with Eqs. (1) and (2).

We calculated the *I. iolas* adult density per patch for each year by dividing the estimated butterfly population size by patch area. It is worth noting that density estimates calculated by dividing population estimates from Eqs. (1) and (2) by patch area were in principle independent of patch area (this last variable is both in numerator and denominator).

Density–patch area relationships can be affected by the intensity of food shortage (Solbreck and Sillén-Tullberg 1990). To obtain an estimate of this variable during the early stages of *I. iolas*, we counted the number of eggs in a maximum sample of 30 fruits per plant in 133, 148, 96 and 133 plants from 24, 27, 21 and 27 patches in 2003, 2004, 2005 and 2006, respectively. Given that one *I. iolas* individual larvae usually requires more than one fruit to complete its development (Munguira 1989), the rate of fruits per egg (the inverse of the number of eggs per fruit) can be considered to be an estimator of food shortage (Solbreck and Sillén-Tullberg 1990).

#### Habitat characteristics

##### *Patch area and connectivity*

For patches consisting of more than one plant, we entered the geographical position of the outermost plants of the patches in the GPS receiver and exported their UTM coordinates to a GIS software package (X-Tools Extension in ARCVIEW GIS, ver. 3.1 for Windows; Environmental Systems Research Institute, Redlands, CA) to calculate areas and centroids. In the case of patches consisting of only one plant, we calculated patch areas from field measures. Given that plant patches were relatively small compared to the geographical area covered by the study system, we estimated distances between patches on the basis of centroids.

We calculated an index of connectivity that take into account the distances of all occupied patches in the system and their sizes. Connectivity for patch  $i$  ( $S_i$ ) was defined as (Hanski 1994b):

$$S_i = \sum p_j \exp(-\alpha d_{ij}) A_j^b, \quad j \neq i$$

where  $p_j$  is the probability of occupancy of patch  $j$ ;  $\alpha$  is a constant setting the distance dependence of migration rate (the slope of the negative exponential dispersal kernel);  $d_{ij}$  is the distance between centroids of patches  $i$  and  $j$ ;  $A_j$  is the area of each patch;  $b$  scales patch areas to population size and emigration rates (Hanski et al. 1996; Moilanen and Hanski 1998; Moilanen 2004). The probability of occupancy equals 1 for occupied and 0 for empty patches when we considered a single year, and it equals the incidence when we considered all years together. Parameter



$\alpha$  is species-specific and describes the dispersal ability of the species. We used a value of 1.5 on the basis of the comparison of *I. iolas* mobility with that of other butterfly species with associated  $\alpha$  values (e.g. Cabeza 2003; James et al. 2003; Schneider 2003). Nevertheless, to test the robustness of analysis, we also calculated connectivities using values of  $\alpha$  of 1 and 2. The parameter  $b$  is defined by two components,  $s$  and  $b'$  (Moilanen 2004):

$$b = s - b'$$

where  $s$  scales patch area to population size, and  $b'$  describes the scaling of emigration rate to patch area. Since the estimated scaling of emigration rate was zero in *I. iolas* females (the individuals that can colonise a patch; results from Virtual Migration model, Rabasa et al. 2007),  $b$  corresponds to the scaling of patch area to population size ( $s$ ). To calculate the empirical value of parameter  $b$ , we fitted the model:

$$PS = aA^b$$

to empirical data, where PS is the estimated peak population size from MRR data in a sample of 13 patches in 2004 (Rabasa et al. 2007),  $A$  is the patch area, and  $a$  is a constant. We obtained  $b = 0.522$  (SE = 0.102), suggesting that population size increases slower than linearly with patch area. Thus, we assume in this paper that  $b = 0.5$ , as has been made in previous studies of butterfly metapopulations (e.g. Hanski et al. 1996).

#### Patch quality

In addition to geometric patch characteristics of the area and connectivity, we considered potential patch quality indicators, such as topographic and microclimate measures (e.g. slope, aspect, surface curvature), and estimated insolation for all 75 patches (only these aspects of habitat quality could be considered). We calculated slope (in degrees), aspect (in degrees from North) and surface curvature (in degrees/100 m) for each patch from a digital elevation model (DEM) at 10-m resolution derived from high-resolution 1:5000 digital maps (5-m contour lines) using ARCVIEW GIS ver. 3.1. We used this resolution because it was fine enough to detect microtopography in the smallest patches but also large enough to prevent large errors during elevation interpolation. The median patch size in the study system was 84.3 m<sup>2</sup>, which is 0.843 the area of one grid cell in the DEM data.

Curvature is an index of the convexity–concavity of a surface at each cell centre (negative, upwardly convex; positive, upwardly concave). For statistical analyses, we transformed the circular variable aspect into a linear north–south gradient (northness) using the cosine transformation on a scale from  $-1$  (south) to  $1$  (north) (Guisan et al. 1999).

We estimated insolation as the total direct solar radiation received per patch during the summer solstice using the SOLAR ANALYST 1.0 extension for ARCVIEW GIS ver. 3.1, based on latitude, slope, aspect and the elevations of surrounding cells. We considered insolation for the summer solstice as a measure of the yearly peak of solar radiation. Insolation was modelled for a  $9 \times 6$ -km<sup>2</sup> area containing the study patches. The value of each topographic/microclimate variable was estimated for each patch as the mean for 10-m grid cells intercepted by the patch surface.

We obtained an estimate of resource quantity measured as average fruit production per plant by counting the number of fruits produced per plant from a sample of plants per patch dependent on patch size (Rabasa et al. 2005). Estimates were made in 24 patches in 2003 and 2005, in 27 patches in 2004 and in 30 patches in 2006.

#### Statistical analyses

We used generalised linear models (GLM) to study the factors determining patch occupancy, incidence and extinction rate of *I. iolas* in the whole 75-patch system. In 2004, 2005 and 2006, there was a small number of vacant patches for analysing occupancy (four, five and seven patches, respectively); consequently, we carried out occupancy analyses for 2003 only. Models included occupancy in 2003, incidence and extinction as dependent variables and patch area ( $\log_{10}$ -transformed), connectivity, slope, northness, curvature and insolation as independent variables. All dependent variables were assumed to have a binomial distribution of errors with logit link function.

The effects of patch characteristics on the density of *I. iolas* ( $\log_{10}$ -transformed) were analysed separately for each year using multiple regression for occupied patches with the complete, available data set. We considered the same independent variables used in GLMs (see above), and the additional variable fruit production per plant in that year as a surrogate of quantity of nectar sources (fruit production is closely correlated to flower production (Rabasa et al. unpublished) and potential oviposition sites. Since adults present during 1 year come from larvae developed in the previous year, we also included fruit production in the previous year as a measure of the quantity of larval resources. This calculation could not be made for 2003 because there was no available information on fruit production in 2002.

A spurious significant relationship between density and patch area would be expected when density is calculated as the ratio of population size to patch area (Lee et al. 2002). Our standard density calculations were in principle independent of patch area (see above [Population size and density](#)). However, a problem could arise from including in the analyses those patches with egg presence and no butterfly records from transects for which we assigned a

minimum population size of 1 (see [Methods](#)) because smaller sites will have higher minimum possible densities (Gaston et al. 1999). Thus, we repeated all analyses excluding these data.

For all analyses, we selected the “best” model which maximised fit but included the minimum number of independent variables using the Akaike’s information criterion (AIC) (Johnson and Omland 2004; Whittingham et al. 2006). To examine for collinearity problems in the models, we calculated all pair-wise correlations between the independent variables and found a relatively strong correlation (Spearman’s rank correlation coefficient  $r_s > 0.3$ ) only between fruit production in 2003 and fruit production in 2004 ( $r_s = 0.651$ ,  $P = 0.001$ ,  $N = 24$ ).

We analyzed the between-year variability in *I. iolas* population size, population density, number of eggs per fruit and fruit production using Friedman’s tests for comparison of multiple-related samples (Zar 1999).

To test the degree of synchrony in the dynamics of local populations and resource quantity, we calculated the temporal correlation of *I. iolas* density and fruit production per plant over the 4-year study period using Kendall’s coefficient of concordance. We also calculated Spearman correlation rank coefficients for *I. iolas* density and fruit production for all pairs of local trajectories over the 4-year period (Kindvall 1996). To test whether there was an effect of distance between patches on the degree of synchrony, we performed Mantel tests (Mantel 1967) between the matrices of pair-wise correlations (Spearman coefficients) and the matrix of distances between patches (measured as Euclidean distances in metres between centroids). In the case of butterfly density, we excluded those patches with extinction events from the calculations of concordance and

correlation coefficients. To test whether the more synchronous patches were those with greater environmental similarity we performed Mantel tests between the degree of synchrony and differences in environmental characteristics between patches (differences in slope, northness, curvature, and insolation) (Sutcliffe et al. 1997).

We performed GLMs and linear regressions using PROC LOGISTIC and PROC REG procedures of SAS ver. 9.0 (SAS Institute, Cary, NC). Correlation coefficients, Friedman’s tests and concordance coefficients were calculated using SPSS ver. 9.0 for Windows. We performed Mantel tests using the Mantel NONPARAMETRIC TEST CALCULATOR for Windows ver. 2.00 (available on <http://www.sci.qut.edu.au/NRS/Mantel.htm>).

## Results

### Occupancy, incidence and extinction

The proportion of occupied patches was relatively high in all years, especially in 2004 and 2006, with 77% of patches (58/75) occupied during the entire 4-year period. Eleven (15%), four (5%), seven (9%) and five (7%) patches remained vacant in 2003, 2004, 2005 and 2006, respectively, and we found no patches permanently vacant during all 4 years. We recorded nine extinction events on nine different patches and 15 colonization events on 13 patches from 2003 to 2006 (Table 1). Of the total of nine extinctions, seven occurred in patches that produced no fruits the year of extinction. Failure in fruit production was related to the accidental burning of one patch in 2005 and to the loss of a large proportion of the aerial part of a single-plant

**Table 1** Descriptive values of occupancy, extinction and colonisation events in 75 patches and mean values ( $\pm$  SD) of adult population size, density and number of eggs per fruit of *Iolana iolas*, and fruit production per plant of *Colutea hispanica* for each study year and for the period 2003–2006

Year	Occupancy	Extinctions	Colonisations	<i>I. iolas</i> population size	<i>I. iolas</i> density (individuals/m <sup>2</sup> )	Number of <i>I. iolas</i> eggs per fruit	Fruit production
2003	0.85	–	–	5.89 $\pm$ 14.62 (27) 6.28 a	0.09 $\pm$ 0.15 (27) 0.09 a	0.08 $\pm$ 0.07 (24) 0.09 b	327 $\pm$ 204 (24) 327 c
2004	0.95	3	10	31.26 $\pm$ 93.79 (30) 37.23 a	0.19 $\pm$ 0.22 (30) 0.15 a	0.82 $\pm$ 0.58 (27) 0.84 b	323 $\pm$ 25 (27) 313 c
2005	0.91	5	1	6.50 $\pm$ 15.35(28) 6.92 a	0.12 $\pm$ 0.17 (28) 0.10 a	0.27 $\pm$ 0.27 (23) 0.27 b	39 $\pm$ 51 (24) 39 c
2006	0.93	1	4	14.50 $\pm$ 50.72 (70) 7.59 a	0.11 $\pm$ 0.15 (70) 0.09 a	0.64 $\pm$ 0.62 (29) 0.65 b	29 $\pm$ 27 (29) 32 c
2003–2006	0.77	9	15	21.59 $\pm$ 60.88	0.12 $\pm$ 0.18	0.48 $\pm$ 0.26	170 $\pm$ 117

Values in parenthesis is the number of patches assessed

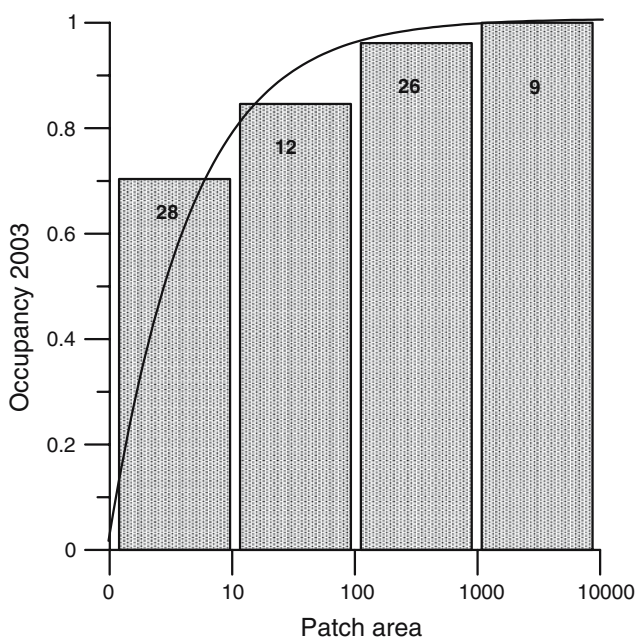
Values followed by lower case letters are mean values calculated from equal-sized samples for the 4 years and are given for comparison (a,  $N = 25$ ; b,  $N = 23$ ; c,  $N = 24$ )

patch in 2004. In the remaining five patches, we observed no apparent cause of fruit failure. Two additional extinctions occurred in patches that produced fewer than ten fruits the year of extinction. Smaller patches were less likely to be occupied by *I. iolas* in 2003 and showed a lower incidence of the species in the period 2003–2006 (Figs. 2, 3). In addition, these had a higher probability of extinction (Table 2, Fig. 4). Modelled data predicted extinction probabilities in the 4-years to be smaller than 0.05 for patches more 100 m<sup>2</sup> in surface area (Fig. 4). Insolation had a significant positive effect on extinction. None of the other variables included in the models had significant effects on occupancy in 2003, incidence or extinction.

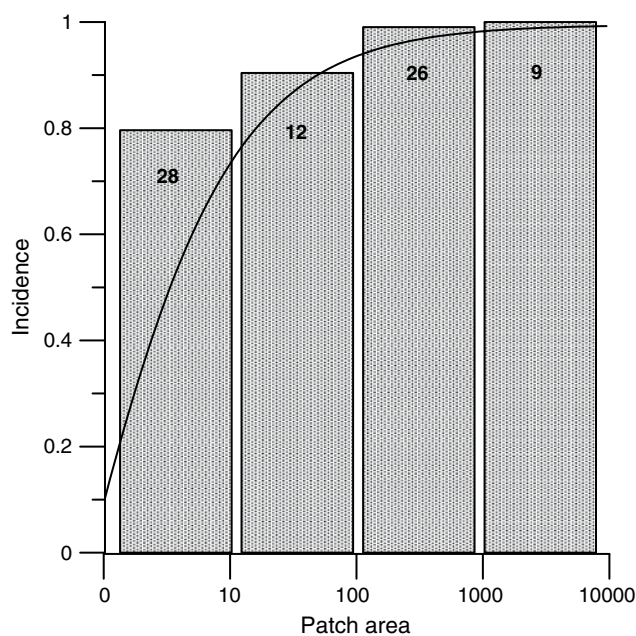
### Population size and density

Population sizes of *I. iolas* (based on occupied patches) varied significantly between years (Friedman test,  $X^2 = 26.51$ ,  $P < 0.001$ ,  $N = 25$ ), being much higher in 2004 (Table 1). The total estimated metapopulation size was approximately 1015 individuals in 2006.

Population densities were also highly variable between years (Friedman test,  $X^2 = 26.51$ ,  $P < 0.001$ ,  $N = 25$ ). Population density was negatively related to area in the four study years (Table 3). In 2004, density significantly increased with increasing fruit production per plant in the



**Fig. 2** Proportion occupied patches by *Iolana iolas* in 2003 (bars) in relation to patch area (m<sup>2</sup>, log<sub>10</sub>-scale) and probability of occupancy modelled using logistic regression (curve). Numbers in bars represent sample sizes. The plotted line is based on the equation in Table 2



**Fig. 3** Observed mean incidence (proportion of years with occurrence) of *I. iolas* during 2003–2006 (bars) in relation to patch area (m<sup>2</sup>, log<sub>10</sub>-scale) and predicted incidence modelled using GLM with binomial error and logit link (curve). Numbers in bars represent sample sizes. The plotted line is based on the equation in Table 2

previous year (2003). No other habitat variable included in the models was significant.

The effects of variables on *I. iolas* density did not change when we excluded those patches with estimated population sizes of 1 (and then with densities dependent on patch area), with the exception that fruit production in 2003 turned non-significant in the model for 2004 ( $P = 0.306$ ; results not shown). On the other hand, the effects of variables on occupancy, incidence, extinction and density did not qualitatively change when we used  $\alpha$  values of 1 and 2 relative to those using  $\alpha = 1.5$  in the connectivity estimates.

The number of *I. iolas* eggs per fruit was particularly small in 2003, of intermediate value in 2005 and large in 2004 and 2006 (Table 1; Friedman test,  $X^2 = 36.49$ ,  $P < 0.001$ ,  $N = 23$ ). Larval food limitation could have been potentially important in 2004, when there were 1.22 fruits per egg on average. Fruit production per plant was relatively high in 2003 and 2004 and approximately one order of magnitude smaller in 2005 and 2006 (Table 1; Friedman test,  $X^2 = 45.55$ ,  $P < 0.001$ ,  $N = 24$ ).

### Synchrony

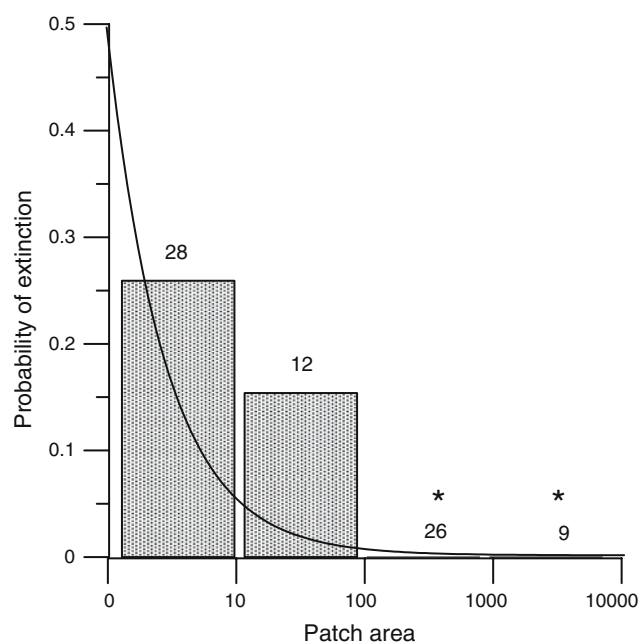
We found a significantly high level of concordance in *I. iolas* density variation among years (Kendall's coefficient,  $W = 0.848$ ,  $X^2 = 81.41$ ,  $P < 0.001$ ,  $N = 4$  years, 25 patches), suggesting that populations fluctuated synchronously. There was also a significant but lower concordance



**Table 2** Generalised linear models for the occupancy in 2003, and incidence and extinction from 2003 to 2006 of *I. iolas* related to patch characteristics, geometry and quality

Model	Variable	Estimate $\pm$ SE	df	Wald $X^2$	P value
Occupancy 2003 $n_o = 64, n_v = 11$	$r^2 = 0.32$				
	Intercept	2.21 $\pm$ 1.42	1	2.39	0.121
	Log (patch area)	1.60 $\pm$ 0.56	1	8.15	0.004
	Slope	-0.18 $\pm$ 0.10	1	2.98	0.084
Incidence (2003–2006)	$r^2 = 0.21$				
	Intercept	0.59 $\pm$ 0.39	1	2.17	0.141
	Log (patch area)	1.56 $\pm$ 0.41	1	14.73	<0.0001
	Curvature	-0.25 $\pm$ 0.18	1	1.96	0.161
Extinction (2003–2006) $n_e = 9, n_p = 66$	$r^2 = 0.44$				
	Intercept	-83.60 $\pm$ 40.91	1	4.18	0.041
	Log (patch area)	-2.22 $\pm$ 0.91	1	5.97	0.015
	Connectivity	-1.08 $\pm$ 0.68	1	2.49	0.115
	Insolation	0.02 $\pm$ 0.01	1	4.30	0.038

Only independent variables included in the “best” models based on Akaike’s information criterion (AIC) are shown. Model parameters are for logit (probability of occurrence, incidence and probability of extinction).  $N = 75$  patches in all cases.  $n_o$ , Number of occupied patches;  $n_v$ , number of vacant patches;  $n_e$ , number of extinct patches;  $n_p$ , number of non-extinct patches



**Fig. 4** Proportion of extinct patches in 2003–2006 (bars) in relation to patch area ( $m^2$ ,  $\log_{10}$ -scale) and probability of extinction modelled using logistic regression (curve) in Table 2. Numbers in bars represent sample sizes. Asterisks indicate that no patches became extinct during the 4-year period in that patch area class. The plotted line is based on equation in Table 2

in fruit production fluctuations during the 2003–2006 period (Kendall’s coefficient,  $W = 0.462$ ,  $X^2 = 42.48$ ,  $P = 0.008$ ,  $N = 4$  years, 24 patches). Pair-wise Spearman’s rank correlation coefficients also showed a high level of synchrony in butterfly density and fruit production among patches,

with mean correlation coefficients of 0.404 and 0.611, respectively. There were no significant relationships between the matrices of correlation coefficients of butterfly density and fruit production against the matrices of Euclidean distances or differences in environmental variables between patches (results not shown).

## Discussion

### Patch occupancy and extinction

The spatial dynamics of *I. iolas* was mostly affected by patch area. Our results are in agreement with those of many studies showing that smaller patches have a lower probability of occurrence and, when occupied, contain populations that have a higher risk of extinction (Hanski and Gilpin 1997; Hanski 1999). Although the modelled extinction rates shown in Fig. 4 are apparently low (lower than 0.05 in 4 years for a 100- $m^2$  patch), it is worth taking into account that these are “realised” rates that include the positive effects of rescue effect (Brown and Kodric-Brown 1977). Given that rescue effect is apparently strong in this system, as deduced from simulation modelling of dispersal (Rabasa et al. 2007), the “intrinsic” extinction rates should be much greater than those shown in Fig. 4.

In the absence of deterministic habitat changes (as apparently was the case of *I. iolas* in this system during the study period), small populations have a higher extinction risk as a result of within- (local) and between-population (regional) processes. Local processes include an increased susceptibility to the pernicious effects of demographic,



**Table 3** Multiple regression models for *I. iolas* density (log-transformed) in 2003, 2004, 2005 and 2006 related to geometric and patch quality characteristics

Model	Variable	Estimate $\pm$ SE	<i>t</i>	<i>P</i> value
Density 2003	$r^2 = 0.81, F = 82.77, P < 0.001, N = 22$			
	Intercept	$-0.47 \pm 0.12$	-3.92	<0.001
	Log (patch area)	$-0.55 \pm 0.061$	-9.10	<0.001
Density 2004	$r^2 = 0.60, F = 16.03, P < 0.001, N = 27$			
	Intercept	$-0.77 \pm 0.20$	-3.86	<0.001
	Log (patch area)	$-0.31 \pm 0.07$	-4.38	<0.001
	Fruit production 2003	$0.001 \pm 0.0003$	2.17	0.041
Density 2005	$r^2 = 0.80, F = 38.58, P < 0.001, N = 22$			
	Intercept	$-0.29 \pm 0.15$	-2.00	0.060
	Log (patch area)	$-0.59 \pm 0.07$	-8.47	<0.001
	Northness	$-0.18 \pm 0.12$	-1.57	0.134
Density 2006	$r^2 = 0.75, F = 24.53, P < 0.001, N = 28$			
	Intercept	$4.37 \pm 3.45$	1.26	0.218
	Log (patch area)	$-0.59 \pm 0.07$	-8.34	<0.001
	Northness	$-0.11 \pm 0.11$	-0.98	0.338
	Insolation	$-0.001 \pm 0.001$	-1.37	0.184

Only variables included in the “best” models based on AIC are shown. The relationship between density and patch area was consistently negative and highly significant for all study years

environmental and genetic stochasticities (Thomas 1994; Hanski 1999), whereas regional processes mostly derive from larger emigration rates (Thomas and Hanski 1997). We found that population size was strongly positively correlated with patch area (but not proportionally to patch area, see [Density patterns](#) below). Population sizes were, on average, small, with only tens of individuals in the “best” years (Table 1), and they were particularly small in the smallest patches, with estimates under ten individuals. This probably makes a large proportion of populations in the study system highly susceptible to demographic stochasticity. We also found some evidence for strong effects of environmental stochasticity, particularly in smaller patches. All extinction events were associated with patches with low or failed fruit production which, in the latter case, inevitably will drive a local recruitment failure of *I. iolas*. Although we were not able to record fruit production for all 75 patches in the system each study year, we did record whether all plants in a given patch failed to produce fruits. Using logistic regression, we found that the probability of fruit failure was negatively related to patch size (estimate  $\pm$  SE =  $-1.453 \pm 0.631$ ;  $P = 0.021$ ), supporting the idea of strong effects of environmental stochasticity in small patches. An additional effect related to small patches could be reduced variability in flowering timing, which could result in few or no fruits being produced in the suitable phenological stage for oviposition. *Iolana iolas* eggs are more likely to be laid on fruits aged 1–2 weeks set at the middle of the flowering period (Rabasa et al. 2005).

In addition to local stochastic processes, regional processes could be also operating in *I. iolas* population dynamics. In an earlier study, we showed that emigration rate decreased with increasing patch area for males and was area-independent for females (Rabasa et al. 2007), which could contribute to increased extinction rates in small populations. However, because immigration rates increased with increasing area, losses by emigration could be compensated or even over-compensated by gains by immigration (for details, see below [Density patterns](#)).

Metapopulation theory states that more isolated patches will have a smaller probability of occupancy due to the decrease in re-colonisation rates with distance (Hanski 1999). We found no evidence for this expectation in the occupancy data for 2003 and the 4-year incidence data. Unfortunately, the high occupancy rates in this system prevent us from analysing colonisation rates. The lack of significant connectivity effects on occupancy and incidence could be a consequence of the relatively long distances moved by *I. iolas* in relation to distances between patches. The longest distance to the nearest patch was approximately 1200 m, whereas the maximum observed distance moved in a mark–release–recapture study was approximately 1800 m (Rabasa et al. 2007). Thus, high recolonisation rates combined with strong rescue effect would result in high patch occupancy and weak effects of connectivity on that variable.

However, this does not mean that connectivity was unimportant for *I. iolas* populations. Two additional lines

of evidence suggest that this variable could be more important in other systems with longer distances between patches: (1) emigration rates have proven to be strongly distance dependent for both males and females (Rabasa et al. 2007); (2) reduced egg incidence has been shown for less connected patches (Rabasa et al. 2005). Further studies in other networks will be required to corroborate the importance of connectivity in occupancy, extinction and colonisation patterns.

### Density patterns

The only consistent pattern with adult density of *I. iolas* across all study years was the negative relationship with patch area. This pattern seems to be common in a wide range of butterfly species (Hambäck et al. 2007; Nowicki et al. 2007). Furthermore, in three of the study years the scaling coefficient was approximately  $-0.5$ , similar to that found for other butterfly studies (Hambäck and Englund 2005). We found no obvious changes of density–area scaling with estimations of food shortage (the inverse of number of eggs per fruit; Tables 1, 3). Although a positive scaling of density with patch area has been generally assumed, negative or non-significant relationships have been also reported, depending on taxa, spatial scale, type of density measured and matrix quality (e.g. Bowers and Matter 1997; Gaston et al. 1999; Connor et al. 2000; Brotons et al. 2003). A negative relationship between density and patch area is expected under the resource compensation hypothesis, based on reduced interspecific competition in smaller patches as a consequence of lower species richness (MacArthur et al. 1972). Although we do not have data to test this hypothesis, it seems unlikely that interspecific competition drives the patch-size dependence of density patterns of *I. iolas*. A more feasible possibility is that negative density–patch area scaling of *I. iolas* could be due to a decreasing density of resources with patch area (Gaston et al. 1999; Gaston and Matter 2002; Matter et al. 2003). In fact, the number of *C. hispanica* plants was significantly correlated with patch area with a scaling coefficient smaller than unity, suggesting that plant density decreased with area:  $\log(\text{number of plants}) = -0.354 + 0.661 \log(\text{patch area})$  ( $r^2 = 0.921$ ;  $P < 0.001$ ;  $N = 75$ ;  $t$ -test for differences of slope = 1,  $P < 0.001$ ). This pattern probably arises from the fact that patch perimeters were defined on the basis of host plant occurrence, which results in increasing amounts of non-habitat areas within patches as area increases in a similar way to that reported for “generalised” individuals–area relationships (Gaston and Matter 2002). Further support for a response of *I. iolas* density to resource density is the fact that we also found a positive relationship with fruit production per plant at least for one of the years (Table 3).

However, with the data available, we cannot tease apart the effects due to reproduction from the previous year from those due to adult habitat use.

In its original formulation, the resource concentration hypothesis stated that a positive relationship between density and patch area results as a consequence of larger emigration rates from smaller patches and larger immigration rates into larger patches (Root 1973). However, it has been recently suggested that the value and sign of density–area scaling can be predicted from local population growth rates and the scaling of emigration and immigration rates with patch area, widening the expectations from the resource concentration hypothesis (Hambäck and Englund 2005). The scaling coefficients for emigration ( $\beta$ ) and immigration ( $\zeta$ ) of *I. iolas* are  $\beta = 0.061$  and  $\zeta = 0.768$  from averaged data of males and females (Rabasa et al. 2007; for  $\zeta$  calculations, see Englund and Hambäck 2007). Assuming the simplest scenario in which local patch processes completely balance, a power law  $\psi = \beta - \zeta$  fully predicts the scale dependence ( $\psi$ ) of the density–area relationship (Hambäck and Englund 2005). Accordingly, the estimated value for *I. iolas* is  $\psi = -0.708$ , which has the same sign but is somewhat greater than any of the observed coefficients shown in Table 3. Thus, we cannot rule out the possibility that patterns of migration scaling in *I. iolas* partly determine the observed density–patch area relationships.

Negative density–patch area relationships could also arise if *I. iolas* individuals escape from predation in small patches with a greater probability than in large patches (the opposite to the standard enemies hypothesis, Brotons et al. 2003). This will be particularly feasible in the case of specialised parasitoids that exhibit metapopulation processes on host networks (e.g. Lei and Hanski 1997). *Iolana iolas* larvae are known to be parasitised by braconid and ichneumonid wasps (Gil-T 2001), but how the parasitism rates change with host population size or host plant area is completely unknown at present.

### Metapopulation dynamics

*Iolana iolas* showed high occupancy rates over the whole 4-year study period (Table 1). In principle, this could suggest that the metapopulation is apparently stable at the short time scale, but this assertion should be taken with caution. For instance, a large-scale extinction was recorded in the seed-feeding bug *Lygaeus equestris* after 10 years of high occupancy rates (Solbreck 1991). Structured models predict that metapopulations with a strong rescue effect may exhibit two alternative stable equilibria, one with most of suitable patches occupied and the other corresponding to metapopulation extinction (Gyllenberg et al. 1997). Metapopulations with this kind

of multiple equilibria may suddenly crash to extinction even in stationary environments (Hanski et al. 1995). This possibility could be exacerbated by the small size of our populations, since the largest one numbered only 490 individuals in the year with higher population sizes (2004).

Although our results on synchrony were somewhat limited with 4 years of data, they do suggest that *I. iolas* density and fruit production fluctuated simultaneously in our study system. With the current data we cannot tease apart the contributions of weather, dispersal and predation in determining synchrony between subpopulations. However, the existence of synchrony is particularly significant to metapopulation systems because this factor is directly related to the likelihood of regional extinction: the more spatially synchronous a metapopulation is, the shorter the expected persistence time (Hanski 1989; Harrison and Quinn 1989; Liebhold et al. 2004).

#### Patch geometry versus patch habitat quality

Of the patch characteristics considered in this study, such as connectivity, topography and microclimate characteristics, patch area appeared to be the most important determinant of *I. iolas* population dynamics. This is in line with Moilanen and Hanski (1998), who found that incorporating habitat quality in modelling metapopulation dynamics of *Melitaea cinxia* did not produce better results than when only area and isolation were used. In contrast, other studies have disagreed on this point and have shown that habitat quality may be more important in determining occupancy, extinction and colonisation patterns than patch area and isolation (Sjögren-Gulve and Ray 1996; Dennis and Eales 1997, 1999; Fleishman et al. 2002).

Dennis et al. (2006) recently criticized metapopulation approaches that identify habitat networks as discrete patches on the basis of vegetation types or host plant presence at the expense of other fundamental requirements of organisms. They suggested that population dynamics can only be completely understood using a definition of habitat based on the distribution of all important resources. The habitat requirements and resources of *I. iolas* are relatively well-known and restricted to *C. hispanica* patches: *C. hispanica* is the only host plant for *I. iolas* larvae as well as being the only nectar plant for adults in our study area; in addition, *C. hispanica* is also used for mate location, resting and other vital activities (Munguira 1989; unpublished data from MRR study). Therefore, for monophagous species as *I. iolas* with clearly delimited resource requirements, patch definition based on host plants seems to be an appropriate approach. This is probably also the case for other metapopulation studies on specialist butterflies with restricted host plants, such as *Cupido minimus* and

*Polyommatus coridon* in Germany (Krauss et al. 2004, 2005). Habitat patch delineation will be probably more difficult to conduct in generalist species with more spatially segregated resources and/or more widespread host plants (e.g. Binzenhöfer et al. 2005), although in those cases a metapopulation approach is less likely to be appropriate. Ultimately, the question of how habitat quality can be incorporated into metapopulation studies can only be answered in specific terms—that is, it should be specifically treated for a particular species and, in some cases, in a particular landscape (Thomas and Hanski 2004).

The results presented here are consistent with our previous findings concerning the relative importance of habitat quality on the dispersal of *I. iolas*, which revealed that patch area and connectivity properly explained the movement patterns on the same habitat network (Rabasa et al. 2007). Nevertheless, there is the possibility that the negligible effects of topographical and climate variables in the study system could be partly due to the particular configuration of host plant distribution. In south-eastern Madrid, typical *C. hispanica* patches are frequently located in steep north-facing slopes (unpublished data). This distributional pattern could result in small among-patches variation in the topographical and microclimate variables. Nevertheless, we only found partial support for this explanation because the coefficient of variation (CV) for patch area was larger than those for slope, aspect and insolation, but not than that for curvature ( $CV_{\text{patch area}} = 259\%$ ;  $CV_{\text{slope}} = 29\%$ ;  $CV_{\text{aspect}} = 54\%$ ,  $CV_{\text{curvature}} = 976\%$ ;  $CV_{\text{insolation}} = 5\%$ ).

Our study illustrates that patch geometry, particularly patch area, explains most of the variation in occupancy, extinction and density of a specialist butterfly with a fragmented distribution. This does not mean that habitat quality is an unimportant factor. Rather, it implies that some differences in habitat quality are subsumed in patch area. Thus, classical metapopulation approaches using only patch area and isolation could be valid for specialist butterflies as *I. iolas*, in which most habitat conditions and resources are associated with host plant patches. Nevertheless, our results are based on data collected from a single network. The importance of the geometric variables versus habitat quality could change in other *I. iolas* networks with different spatial structure and/or under different conditions. The extent of these potential sources of variation should be the subject of future research.

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