Conservation ecology of the endangered Iolas blue *Iolana iolas* (Lepidoptera, Lycaenidae): enhancing monitoring schemes and habitat restoration

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Abstract

The dramatic decline in distribution and abundance of numerous insect species requires evidence-based conservation action. We investigated the efficiency of a population restoration programme aimed at reducing the risk of extinction of the Iolas blue in Switzerland. We assessed species' habitat selection, detectability, demography and dispersal ability. Weekly count surveys performed at 38 plantations dedicated to the species' unique host plant (bladder senna, *Colutea arborescens*) resulted in an occupancy rate of 50%, with mostly very low relative abundance indices. The site-occupancy habitat analysis demonstrated that species abundance was best explained by host plant vitality (intensity of blossoming and number of seedlings), habitat patch connectivity and solar radiation. Capture-mark-recapture surveys conducted at four sites confirmed the large variation in local population sizes, yielded a very high catchability (82%) and individual detectability (86%), and revealed an average adult life expectancy of 3.6 days. Seventy-eight percent of dispersal events were within 550 m (maximum of 1490 m), with significantly higher dispersal frequency and longer dispersal distances in females. Our results first set the basis for future efficient count surveys to assess species distribution and abundance. Second, they provide evidence-based recommendations to enhance habitat restoration, which includes two main operations. First, the attractiveness of bladder senna plantations must be enhanced by promoting mass blossoming, which can be achieved through systematic autumn pruning of the extant plantations and the creation of new plantations at the most profitable sites for the plant. Second, these new plantations should be placed in the major identified gaps within the landscape matrix in order to improve metapopulation connectivity. The implementation of these prescriptions would decrease the risks of extinction of the last population of *Iolana iolas* in Switzerland.

278 words

Keywords: *Colutea arborescens*, dispersal, ecological restoration, habitat variable, Switzerland, vineyard

Introduction

The protection and management of semi-natural areas is crucial to prevent biodiversity erosion in human-used ecosystems. However, semi-natural habitats of conservation concern are often heavily damaged and strongly fragmented, which calls for biodiversity management operating beyond simply setting aside land as preserves (Naughton-Treves *et al.*, 2005; Sinclair *et al.*, 1995). Ecological restoration is hence often necessary to assist in the recovery of a threatened population or species (Schaub *et al.*, 2009; Schultz & Crone, 2005; Sinclair *et al.*, 1995), which requests a detailed knowledge of its ecological requirements (Hirzel *et al.*, 2004; New, 2007; Settele & Kühn, 2009).

As other plant and animal taxa, insects of semi-natural habitats currently face very high extinction risks, principally due to changes in land-use and management practices that lead to habitat degradation and fragmentation (Robinson & Sutherland, 2002; Thomas & Morris, 1994; Thomas *et al.*, 2004). Among insects, butterflies represent a well-studied group, and are therefore frequently used as surrogates when assessing general trends in biodiversity (Altermatt *et al.*, 2008; Erhardt, 1985; Kéry & Plattner, 2007; Thomas, 2005; Van Swaay *et al.*, 2006). Not surprisingly, butterflies are the subject of several habitat restoration programmes, especially in agricultural landscapes.

An ecological restoration programme of a rare butterfly species threatened with extinction in Switzerland was started in 2000 (Sierro, 2007). In the past decades the Iolas blue (*Iolana iolas,* Lycaenidae) had underwent a slow and continuous population decline in Central Valais, the last inhabited area in Switzerland (Carron & Praz, 1999). The expansion of vineyards and human settlements had been identified as the main cause for its rarefaction (Sierro, 2007). In order to enhance habitat quality for the butterfly, seedlings of bladder senna (*Colutea arborescens,* Fabaceae), its unique host plant in Switzerland, were opportunistically planted at numerous locations, mostly within vineyards (Sierro, 2007). Whenever possible the plantations were situated close to sites where Iolas blue was detected during former surveys (Carron & Praz, 1999). This resulted in the plantation of 1-12 seedlings originating from local shrubs at 38 sites between 2000 and 2006 (Sierro, 2007).

The main goals of this study were to develop guidelines for effective population monitoring schemes, and to evaluate the efficiency of the so far implemented habitat enhancement measures in order to propose a set of adjusted evidence-based recommendations to improve the restoration programme. More specifically, we first studied habitat requirements of *Iolana iolas* to inform management about best practices (Bergman, 1999; Lambeck, 1997; Thomas, 1991). Weekly count surveys were carried out to estimate both relative population abundance and species-habitat associations. Second, we performed capture-mark-recapture (CMR) experiments at four sites to draw basic information about absolute population sizes and demographic rates (Lande, 1988) in order to predict patterns of species persistence in a heavily fragmented semi-natural agricultural landscape (Schtickzelle *et al.*, 2002). These experiments additionally provided information about species catchability and life expectancy. We then combined data from the count surveys and CMR experiments to provide a first estimate of individual detectability, assuming an individual is present in the population at the time of the survey (MacKenzie & Royle, 2005). This information would be crucial to construct future efficient monitoring schemes (MacKenzie *et al.*, 2003; Pellet, 2008; Pollock *et al.*, 2002) because not accounting for imperfect detectability inevitably leads to underestimating population abundance and site occupancy (MacKenzie & Royle, 2005). Finally, we analysed the dispersal capacity of Iolas blue to assess both the extinction risk of the regional metapopulation and its ability to recolonise isolated habitat patches once deserted (Hanski, 1999).

Material & Methods

Study species

The Iolas blue (Ochsenheimer 1816) is widespread throughout southern Europe (listed as near threatened in the European red list (Van Swaay *et al.*, 2010)) and the Maghreb but usually occurs very locally (Tolman & Lewington, 2008). The Swiss population is isolated from all other European populations and is restricted to an area of approximately 21 km^2 in Central Valais (Carron & Praz, 1999). A strong decline in both distribution and abundance, following the degradation of its habitat, led to Iolas blue being one of the rarest butterflies in Switzerland (Sierro, 2007). The species has been listed as endangered in the Swiss Red List (Gonseth, 1994) and classified among species with highest conservation priority (Carron *et al.*, 2001).

The species is univoltine, with a flight season between May and late July (Tolman & Lewington, 2008). The principal larval host plant is bladder senna or, depending on the region, other members of the genus *Colutea* (García-Villanueva *et al.*, 1996; Munguira & Martín, 1993; Tolman & Lewington, 2008). Bladder senna is a leguminous, nitrogen-fixing and perennial shrub (De Andres *et al.*, 1999). It can reach a height of four meters and has characteristic yellow flowers and bloated fruits (Lauber & Wagner, 2001). The shrub is native in the Mediterranean basin (De Andres *et al.*, 1999) and inhabits the warmest and driest hillsides up to 1000 m above sea level in Valais (Sierro, 2007). Females of Iolas blue lay their eggs on the seed-capsules or in the calyx, and caterpillars feed exclusively on the fresh, green seeds (Tolman & Lewington, 2008). Iolas blue hibernates as a pupae underneath a stone (Benz *et al.*, 1987; Tolman &

Lewington, 2008). Myrmecophily has been suspected by Tolman & Lewington (2008), but could not be demonstrated so far (Gil-T., 2004)

Study area

The study was conducted in Valais (southwestern Switzerland, 46.3 °N, 7.3 °E). All surveyed 38 bladder senna plantations were located along the south-exposed hillside of the Rhône valley between 500 and 950 m altitude, spreading over an area of approximately 10 km^2. Up to 800 m altitude the area is dominated by terraced vineyards (~80% of land cover). Unimproved areas like hedges, xeric woodland and steppe grassland are rare below 800 m, whereas meadows and xeric deciduous forests (~70%) become dominant above this elevation.

Sampling design

Count surveys

Count surveys were performed during the whole duration of the flight season (late May – late July) in order to determine both the site occupancy rate and the relative population abundance, this by applying the Pollard index (Pollard, 1977). All 38 bladder senna plantations were surveyed at least once a week between 9.30 am and 5.00 pm under good weather conditions [temperature above 18 °C (Sierro, 2007), wind speed below 3 Bf and a minimum of 80% sunshine during the survey (Koordinationsstelle Biodiversitäts-Monitoring Schweiz, 2008)] (Pollard, 1977). On average, a plantation survey lasted 10 min during which the number of observed Iolas blue in a 5 m radius around the plantation patch was recorded.

Habitat analysis

We selected 10 habitat variables (see Table 1) believed to influence at least one of Iolas blue's life history stages and to bear some predictive power regarding observed abundances drawn from Pollard indices. Although we focused on variables representing high management potential such as blossom intensity, presence of stone walls, bare ground and stone cover underneath the bladder sennas, other intangible variables (e.g. number of seedlings of bladder senna or solar radiation) were also included (Carron & Praz, 1999; Sierro, 2007). Variables were measured either in the field or in arcGIS (www.esri.com, Environmental Systems Research Institute, California). Given the occurrence of Iolas blue up to approximately 1000 m a. s. l. in the study area, we also tested for an effect of the altitude of the plantation (Sierro, 2007) determined with GPS (etrex summit, GARMIN Ltd, USA). The potential myrmecophily suggested by Tolman & Lewington (2008) was assessed by quantifying the abundance of *Tapinoma erraticum* in each plantation. Twenty 2 ml Eppendorf tubes, filled with sugared water on cotton, were randomly distributed on the ground within each plantation. Tubes were collected after one hour, with the number of tubes containing at least one *T. erraticum* used as an index of abundance.

As a combination of habitat patch area and connectivity has been demonstrated to be a good proxy of site-occupancy for butterflies in general, we incorporated such a metric in our habitat analysis (Hanski *et al.*, 1995; Pellet *et al.*, 2007; Thomas *et al.*, 1992; Wahlberg *et al.*, 1996), referring to Hanski (1994b; see Table 1). Habitat area was estimated from the number of flowers per plantation (thereafter referred to as blossom intensity). For this purpose we weekly estimated the number of flowers for each bladder senna during the whole flight season of *Iolana iolas.* Finally, the values for all the shrubs within one plantation were summed up. The occurrence of a stone wall and the visual estimates for stone and bare ground cover, all considered as positively influencing *Iolana iolas* (Benz *et al.*, 1987; Carron & Praz, 1999; Tolman & Lewington, 2008), were performed within 3 m radius of a bladder senna, this being the maximum expected moving distance of caterpillars. Values for stone and bare ground cover were averaged for each plantation whereas the occurrence of a stone wall was denoted as present if at least one stone wall was closer than 3 m to the next bladder senna. We determined the number of bladder sennas higher than > 1 m because only larger bladder sennas are supposed to be attractive for Iolas blue (Carron & Praz, 1999). The number of bladder senna seedlings was also counted in a 5 m radius (99% of dispersal range of seeds Vittoz & Engler, 2007) around each plant to test for converging habitat preferences in the plant host and the butterfly, and to assess the degree of natural rejuvenation within plantations. As our butterfly population is situated at the northernmost border of its distribution, we expected a preference for sites warmer than average. We tested for such an association by using solar radiation as a proxy for climatic conditions: the data was extracted from GIS databases for each of the 38 study sites.

Capture-Mark-Recapture (CMR)

In order to estimate individual demographic parameters, we performed capture-mark-recapture (CMR) experiments at four sites (2 plantations and 2 naturally occurring bladder senna stands) which had harboured large population sizes over the past years (A. Sierro, unpublished data).

CMR experiments were conducted under the same weather conditions as count surveys (see above). On each CMR session, all Iolas blue were hand-netted, sexed, and individually marked on the underside of the hind wings with a permanent pen, and released immediately after manipulation. On subsequent sessions, we only re-netted those individuals that could not be visually identified from a distance. Each sampling session lasted until all detected individuals were either marked or identified, which usually occurred within 30-45 min. Sampling sessions were repeated every second to third day, time and weather permitting. An individual capture-history consisting of 1 (captured) and 0 (non-captured) was produced for each marked individual (Nichols, 1992).

Dispersal analysis

An analysis was performed to obtain estimates about the dispersal ability of Iolas blue. It included all Iolas blue from the CMR experiments plus those which had been haphazardly hand-netted on any other occasion in the field. All the captures and recaptures were localized with GPS (etrex summit, GARMIN Ltd, USA) with a 5-10 m accuracy.

Statistical analyses

Count surveys

Count survey data were used to calculate the percentage of occupied plantations and the corresponding Pollard index, which is defined as the sum of the mean weekly counts (Pollard, 1977, 1982) per plantation.

Habitat analysis

Generalized linear models (GLM) were run in software R 2.12 (R Development Core Team, 2010) to test which habitat variables affected the abundance of Iolas blue. We tested a total of 11 models, including 9 a priori defined models, as well as the full model (model # 2, that includes all variables) and the intercept model (model # 1) (Table 2). Model # 3 follows the area-isolation paradigm of metapopulation dynamics and, hence, incorporates only the variables blossom intensity and habitat patch (i.e. plantation) connectivity (Hanski *et al.*, 1995; Pellet *et al.*, 2007; Thomas *et al.*, 1992; Wahlberg *et al.*, 1996). Model # 4 is a slight extension of model 3 and was built to test if, taking connectivity and blossom intensity into account, the quantity of bladder senna within a plantation influences the abundance of Iolas blue. In model # 5 the focus was on a combination of connectivity and vitality of bladder senna. A continuation of this model was model # 6 where we dropped the metapopulation variable connectivity and replaced it by the quantity of bladder senna per plantation. Shifting the focus from bladder senna back to Iolas blue, we then built model # 7 and incorporated those habitat variables that were supposed to influence the different life stages of Iolas blue most strongly. Blossom intensity is supposed to influence mainly adult Iolas blue, but given its very high correlation (r = 0.95) with fruit number it reflects the quantity of resources available for caterpillars as well (Rabasa *et al.*, 2007, own unpublished information) whereas ant abundance and stone cover are assumed to positively influence the pupation process (Benz *et al.*, 1987; Tolman & Lewington, 2008). Model # 8 focuses on pupation, and includes therefore the variables ant abundance, stone wall, stone and bare ground cover. Model # 9 considers only the circumstances on the ground at each plantation. Model # 10 considers the location of the plantation in the wide landscape and the size of the plantation (quantity of bladder senna bushes). Model # 11 informs about the combined importance of altitude, habitat connectivity and solar radiation.

We checked for cross-correlations between habitat variables. No pair of variable had a coefficient $r > |0.6|$; all were thus retained for the analyses. The 11 habitat models were then tested using the glm function in R. Our sampling units were the 38 plantations. Pollard indices were used as dependent variables whilst habitat variables were our independent variables. The error was assumed to be Poisson distributed, which implied fitting a log-link function. We used an information theoretic approach for model classification. Models were ranked by their decreasing AIC_C, which is an adaptation of the Akaike selection criterion advocated for small samples, specifically when the number of parameters exceeds the sample size divided by 40 (Burnham & Anderson, 2004; Johnson & Omland, 2004). Models with $\Delta AIC_C \leq 2$ were considered as having substantial support (Burnham & Anderson, 2004). In addition, AIC_C weights ($wAIC_C$), which indicate the relative support of a model (Burnham & Anderson, 2002), and pseudo-R^2 (Veall & Zimmermann, 1996), were calculated for each model.

To control for any bias induced by the very high Pollard index obtained at the most densely inhabited plantation (Caucagne/St-Léonard), the whole procedure was repeated while omitting this outlier. As results were similar, we report only on models including all study sites.

Capture-Mark-Recapture (CMR)

CMR data was analysed using the POPAN formulation of the Jolly-Seber approach in software MARK 6.0 (White & Burnham, 1999). This formulation accounts for open populations (typical of insects populations) and allows not only to estimate capture rates and individual survival, but also recruitment (Schtickzelle *et al.*, 2003; Schwarz & Arnason, 1996). It is assumed to be the most robust approach to analyse butterfly population dynamics (Haddad *et al.*, 2008; Schtickzelle *et al.*, 2003). CMR data of all four sites were analysed separately. For each site eight models were built, with apparent daily survival (Φ), catchability (p) and recruitment (probability of entering the population through immigration or birth) (p_{ent}) being either constant (denoted [.]) or time-specific (denoted [t]), using a parameter specific logit link function. Models were ranked with the same theoretical information approach as above. However, estimates of the apparent daily survival were model-averaged (Johnson & Omland, 2004) and used to calculate the life expectancy (l= -1/ln(Φ)) (Mallet & Barton, 1989).

Individual detectability was computed as the ratio of daily counts (C_i) on the corresponding daily population size (N_i) estimated by CMR for the Caucagne/St-Léonard plantation.

Dispersal analysis

Dispersal rate was defined as the proportion of individuals recaptured at a distance of more than 40 m at least once during another capture event (Rabasa *et al.*, 2007). To compare the average dispersal distances between sexes a Mann-Whitney-test was used.

Results

Count surveys

Iolas blue was observed at 19 out of 38 plantations, which gives an occupancy rate of 50%. Pollard indices for the different plantations were generally very low (between 0 and 15), with the noticeable exception of the Caucagne/St-Léonard plantation, where an index of 50 was obtained (see Fig. 1).

Habitat analysis

The ranking of the 11 tested models revealed the existence of one best model explaining the abundance of Iolas blue (see Table 2). This model (AIC_C weight of 0.206) includes the variables connectivity, blossom intensity and number of seedlings, which are all positively related to the abundance of Iolas blue, plus the variable solar radiation that has a negative influence. The second best model (ΔAIC_C = 2.661 and $wAIC_C$ = 0.180) includes connectivity and blossom intensity, both again positively related to abundance. The *pseudo*-R^2 values are high for both models (83.3% and 81.0%, respectively).

Capture-Mark-Recapture (CMR)

The best model for all sites included constant survival, constant catchability and time-specific emergence rates {Φ(.) p(.) p_{ent}(t) N(.)}. Estimates for apparent daily survival (± standard error) were between 0.70 (±0.08) and 0.83 (±0.05), translating into a relatively short average life expectancy of 3.63 (±0.35) days. Model-averaged daily catchability was between 0.82 (±0.09) and 1.00 (±0.00), the latter drawn from a small population in which all individuals were captured at each session. The model-averaged recruitment rates were between 0.06 (±0.02) and 0.17 (±0.10). Total population sizes (N_{tot}) were between 12 (±0) and 92 (±0) (see Table 3). Note that the very small standard errors are a by-product of a very intensive sampling effort in all four populations and not an artefact.

It has to be noted that for plantation Caucagne/St-Léonard, the model {Φ(t) p(.) p_{ent}(.) N(.)}, which assumes a time specific apparent daily survival (Φ) but a constant catchability (p) and recruitment (p_{ent}), couldn't be tested because no convergence was reached. For the other sites all models could have been tested but some had to be ignored in the final comparison because they only led to spurious results.

The comparison between daily counts (C_i) and the corresponding estimate of daily population size (N_i) resulted in a high individual detectability of 0.86 (±0.39).

Dispersal analysis

During the whole flight season 180 Iolas blue were netted and marked, with a sex ratio significantly biased towards males (males: 105, females: 75, χ^2-test, df = 1, χ^2_{Yates} = 4.76, $P < 0.05$). Overall, 69 individuals (38%) were recaptured at least once with again a significantly higher proportion of males (males: 49%, females: 24%, χ^2-test, df = 1, χ^2_{Yates} = 10.16, $P < 0.01$). From all the observed movements, 22% and 42% for males and females, respectively, were considered as dispersal events (> 40 m distance; χ^2-test, df = 1, χ^2_{Yates} = 3.87, $P < 0.05$). The distances of these movements also differed significantly between sexes with, a median of 270 m for males and 698 m for females (Mann-Whitney-test, z = 2.62, $P < 0.01$) (see Fig. 2). Most (78%) dispersal distances were shorter than 550 m, with a maximum distance of 1490 m.

Discussion

This study shows some success in the occupancy of the bladder senna plantations by the rare Iolas blue in Valais. However, as the corresponding Pollard indices were very low for all 38 plantations but one, the vast majority of local populations were highly exposed to demographic stochasticity. Habitat suitability models revealed that the abundance of this butterfly is best explained by the blossom intensity within a plantation and the location of a plantation within the metapopulational landscape. The number of bladder senna seedlings and solar radiation also influenced Iolas blue abundance, but to a much lesser extent. Capture-mark-recapture (CMR) experiments indicated a much shorter life expectancy than expected based on species' body size and life history (Beck & Fiedler, 2009; Lindzey & Connor, 2010; Vandewoestijne *et al.*, 2008). They also revealed a very high catchability and individual detectability, at least under standardized survey conditions as applied here. Clear differences between sexes concerning dispersal capacity confirmed former findings from Spain (Rabasa *et al.*, 2007): females perform twice as many dispersal trips as males, covering on average much longer distances than males. All these results have implications for population management that we are detailing hereafter.

Count surveys

Four to ten years after having been planted for Iolas blue, half of the bladder senna plantations were occupied by the targeted butterfly, which demonstrates species' ability to colonise newly created habitats rather quickly (Carron & Praz, 1999). However, most populations were small and we could assess both local extinctions and local colonization events, i.e. a high susceptibility to demographic stochasticity. This situation clearly calls for a metapopulational approach to guide conservation effort.

The largest population occurred in the Caucagne/St-Léonard plantation, harbouring almost 50% of the entire surveyed metapopulation. Its Pollard index was four times higher than in the second most abundant population, indicating a huge contrast in plantations occupancy. This numerous population probably functions as a source in our metapopulation system (Pulliam, 1988), with all others appearing as extremely vulnerable. It is therefore urgent to protect this source population and to gain new source populations in the area.

Habitat analysis

Several butterfly studies best described patterns of patch occupancy using an area-isolation paradigm of metapopulation dynamics (Hanski *et al.*, 1995; Pellet *et al.*, 2007; Thomas *et al.*, 1992; Wahlberg *et al.*, 1996), whereas others simply stressed the importance of habitat quality and resource abundance (Dennis & Eales, 1997, 1999; Dennis *et al.*, 2006; Fleishman *et al.*, 2002; Thomas *et al.*, 2001). Our analysis focused on abundance (rather than mere presence/absence of the butterfly within a plantation) and included variables expressing both metapopulation structure (patch area and connectivity), and habitat quality and resource abundance (e.g. blossom intensity, among other descriptors). Our best model for species-habitat associations consisted of only four predictors, demonstrating the importance of both connectivity and habitat quality / resources abundance. Connectivity is more likely to influence abundance when the fraction of immigrants is large (Matter *et al.*, 2003), which may explain its prime importance in our study. Many investigated populations, especially the spatially better connected plantations, probably resulted from colonization by immigrants which may even have rescued some populations after extinction (Moilanen & Nieminen, 2002). The blossom intensity varied by 2 orders of magnitude between occupied plantations. Its crucial role is not surprising. First, *Colutea* flowers are believed to be an almost exclusive nectar source for adult Iolas blue (Rabasa *et al.*, 2008) although Carron & Praz reported additional feeding on *Sedum album* and *Geranium sanguineum* (pers. comm.). Second, blossom intensity correlates with the quantity of fruits (Rabasa *et al.*, 2007, own unpublished information), the latter being the exclusive diet of caterpillars (Tolman & Lewington, 2008). We also noticed that a high blossom intensity generally correlates with a long flowering season, which leads to a staggered emergence of fruits. This warrants a lasting availability of a bulk of attractive young fruits that may stimulate both oviposition and larval development (Rabasa *et al.*, 2005). The negative influence of solar radiation is intriguing and, on a first glance, rather counter-intuitive given the mostly southern distribution of *Iolana iolas*. Solar radiation might impact Iolas blue abundance either directly or indirectly. First, *Iolana iolas* apparently shows little tolerance to heat, as established from a Spanish CMR experiment (Rabasa, pers. comm.). Second, hot conditions may negatively affect the breeding performance of bladder senna. Even though this bush belongs to the wide Mediterranean basin (De Andres *et al.*, 1999), we could observe how rapid are flowering and fruit ripening during warm spells, which probably contributes to diminishing both foraging opportunities for the imagines and fruit palatability for the larvae.

The positive influence of bladder senna seedlings on Iola blue abundance could be explained by converging abiotic habitat preferences in the two species. Natural regeneration of the host plant can be a strong stimulus for habitat selection in the butterfly, which may so foresee the future reproductive potential of a site. Alternatively, germination of *Colutea* requests bare ground, a habitat characteristic also indispensable for Iola blue pupation. However, this latter interpretation must be taken with caution because neither bare ground nor stone cover were included in our best models (Table 2).

Capture-Mark-Recapture

There is some controversy about the relevance of CMR studies for conservation biological studies of endangered butterflies. CMR experiments are very demanding (Haddad *et al.*, 2008), marking can damage butterflies (Murphy, 1987), alter their behaviour and therefore recapture probabilities (Singer & Wedlake, 1981). This may potentially generate erroneous population estimates, especially when sample size is small (Haddad *et al.*, 2008). In our study, however, we did not notice any such detrimental effects. The relatively large body size of Iolas blue, combined with few re-netting events may have contributed to this success. Notwithstanding other drawbacks, we obtained acceptable estimates in all research directions.

First, we were able to provide population size estimates for the four presumably largest remaining Iolas blue subpopulations in Switzerland, confirming its red list status and assessing its high susceptibility to demographic stochasticity, i.e. the necessity to continue and enhance habitat restoration. The study also establishes the disproportionate importance of one single plantation for the survival of the whole metapopulation and sets the basics for future cost-effective monitoring schemes, although we have to keep in mind that both within-season, weather-dependent, as well as between-years population fluctuations may be large in butterflies (Rabasa *et al.*, 2007).

Second, the average life expectancy of adults was much lower than the initially expected two weeks (Rabasa, pers. comm.), but still comparable to the lowest values obtained from other CMR run on 24 species of Lycanidae (4-7 days in non-hibernating adults; (Beck & Fiedler, 2009; Meyer-Hozak, 2000; Thomas *et al.*, 2010). Yet, this short lifespan may have resulted from exceptionally adverse weather conditions during one week in the middle of the flight season in 2010, followed by an extraordinary warm and dry spell, a violent contrast potentially harmful for imagines (Mattoni *et al.*, 2001; Thomas *et al.*, 2009). Given life expectancy and the fact that each individual should be available for capture 3-4 times to allow powerful CMR modelling (Pellet & Gander, 2009), we suggest future CMR experiments be repeated daily or every second day, under suitable weather circumstances.

Third, catchability (0.82 – 1) and individual detectability (0.86) were very high, as a result of a large body size, conspicuous colour and male typical patrolling behaviour. Habitat openness (vineyards) and surveys restricted to warm and sunny days have further contributed to these high probabilities. Based on these considerations, a brief, 10 min survey per plantation would be enough to estimate daily abundance through counts.

Based on these considerations, for future monitoring schemes we advocate a hybrid approach with short-term local CMR experiments combined with frequent count surveys of all plantations according the protocol used here.

Dispersal analysis

An observed sex ratio biased towards males is typical in butterfly surveys (Wahlberg *et al.*, 2002). In our study, a focus on bladder senna plantations may one the one hand have enhanced the detectability and therefore capture of patrolling males; one the other hand, it may have caused us to miss females that have a greater propensity to disperse (Baguette *et al.*, 1998; Carron & Praz, 1999; Cizek & Konvicka, 2005; Välimäki & Itämies, 2003; Wahlberg *et al.*, 2002). A common strategy among female butterflies consists in distributing offspring over several patches for reducing mortality or parasitism (Petit *et al.*, 2001; Välimäki & Itämies, 2003), a tactic that would be beneficial for Iolas blue because of the high spatial and temporal variability in host plant fruiting (Rabasa *et al.*, 2008) and pressure exerted on larvae by parasitic ichneumonid wasps (Gil-T., 2001).

The sexes differed in their dispersal ability, in line with the findings of Rabasa *et al.* (2007), except as regards dispersal range. The same explanation as above may explain the pattern, assuming spatial autocorrelation in parasites pressure and local catastrophes. However, the species seems to have a limited dispersal capacity with only 7 trips (22%) beyond 550 m. A strongly skewed distribution of dispersal distances, with only few individuals flying long distances (maxima of 1490 and 1792 m, in this study and Rabasa *et al.* (2007), respectively), is commonly observed in butterflies (Brommer & Fred, 1999; Gutiérrez *et al.*, 1999; Wahlberg *et al.*, 2002). In addition to the high emigration rates observed in females, this renders a colonisation of isolated bladder senna plantations very unlikely if interpatch distances are greater than ca 1-2 km. Conservation efforts should thus focus mostly on restoring a rather fine-grained suitable habitat matrix in the wider landscape.

Implications for conservation

The ecological restoration program launched in 2000 was instrumental in securing medium term viability of the last Iolana iolas population of Switzerland. More concerted efforts are now needed to guarantee its long-term persistence. We present a conservation road map based on our current knowledge of species' ecology.

The main core population must receive a special protection status and its importance must be clearly explained to local stakeholders. The attractiveness of this and other extant plantations must be enhanced in order to host larger populations.

A first series of measures consists in increasing blossom intensity. Limiting herbicide application in marginal bushy areas around vineyards would be a major obvious contribution. Although this measure may be difficult to implement on a wide scale, convincing viniculturists who have accepted bladder senna bushes on their land is probably a promising approach. Regular pruning outside the vegetation period would be another cost-efficient way to promote bladder senna blooms. Finally, irrigation of plantations from water pipes devoted to vineyard irrigation may further boost flowering (De Andres *et al.*, 1999).

A second series of measures is to increase the metapopulation capacity of the landscape by increasing habitat connectivity in the vineyard-dominated matrix (Hanski & Ovaskainen, 2000). This must be achieved by planting new patches of at least 20 large bladder senna within 550 m of an existing population. Plantation sites should be neither too hot nor too dry, and the underlying idea would be to create new large source populations. This is the only way to reconnect all subpopulations in Central Valais, to minimize the risk of local extinctions without re-colonisation (Hanski, 1999) and to raise the buffer capacity against potentially adverse land-use changes to come (Settele & Kühn, 2009).

Through the identification of several factors limiting site occupancy and habitat suitability, this study provides the first set of evidence-based guidelines to improve conservation action of the last remaining Swiss population of the Iolas blue in an efficient and effective manner.

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Tables

Table 1: Description of the habitat variables recorded for modelling Iolas blue abundance

Variable	Measurement	Mean ± SD	Min.	Max.
Altitude	m above sea level	680.4 ± 120.6	521	948
Ant abundance	Number of traps out of 20 per plantation containing *Tapinoma erraticum*	4.1 ± 4.4	0	16
Connectivity	$S_i = \Sigma\, p_j \exp(-d_{ij})$ (Hanski, 1994)	3.3 ± 1.5	0	5
Stone wall	Presence/absence of a stone wall within 3 m radius around a bladder senna	-	-	-
Blossom intensity	Sum of weekly counts of the absolute number of bladder senna flowers in a plantation	3’262 ± 5’110	21	28’545
Bare ground cover	Percent area of non-vegetated ground within 3 m radius around a bladder senna	44.2 ± 23.5	5	95
Bladder senna seedlings	Number of *Colutea* shrubs younger than the plantation itself within 5 m radius around a bladder senna bush (Vittoz & Engler, 2007)	8.1 ± 13.0	5	56
Bladder senna quantity	Number of bladder senna > 1 m height per plantation	4.8 ± 6.3	1	28
Solar radiation	W/m^2	237’458 ± 132’876	25’479	535’448
Stone cover	Percent area covered with stones (> 5 cm diameter) within 3 m radius around a bladder senna	16.7 ± 15.7	0	55

Table 2: Selection of candidate models for Iolas blue abundance. Models are ordered by decreasing AIC_C. The sample size (*n*) is 38 for all models, *K* is the number of parameters.

#	Model	*K*	AIC_C	ΔAIC_C	$wAIC_C$	Deviance	*pseudo-R^2(%)*
5	*N*(connectivity + bloom + seedlings + solrad) *p*(.)	5	124.635	0.000	0.206	58.664	83.3
3	*N*(connectivity + bloom) *p*(.)	3	127.296	2.661	0.180	66.489	81.0
4	*N*(connectivity + bloom + senna.quantity) *p*(.)	4	129.722	5.087	0.160	66.408	81.1
7	*N*(ant + bloom + stone) *p*(.)	4	130.142	5.507	0.156	66.835	80.9
2	*N*(altitude + ant + connectivity + stone.wall + bloom + bare.ground + seedlings + senna.quantity + solrad + stone) p(.)	11	130.874	6.239	0.151	44.620	87.3
6	*N*(bloom + seedlings + senna.quantity + solrad) *p*(.)	5	142.185	17.550	0.086	76.207	78.3
10	*N*(altitude + connectivity + senna.quantity) *p*(.)	4	161.632	36.997	0.032	98.324	72.0
8	*N*(ant + stone.wall + bare.ground + stone) *p*(.)	5	210.325	85.690	0.003	144.350	58.8
11	*N*(altitude + connectivity + solrad) *p*(.)	4	248.352	123.717	0.000	185.040	47.2
9	*N*(stone.wall + bare.ground + seedlings + stone) *p*(.)	5	275.435	150.800	0.000	209.460	40.2
1	*N*(.) *p*(.)	1	406.751	282.116	0.000	350.540	0.0

Table 3: Estimates (±SE) for apparent daily survival (*Φ*), catchability (*p*), probability of entering the population (p_{ent}) and total number of butterflies that ever were present in the study population (N_{tot}). Estimations based drawn from the model {*Φ*(.) *p*(.) $p_{ent}(t)$ *N*(.)} applied at for four sites. Values for p_{ent} and the corresponding standard errors are averaged for each site.

site	*Φ* ± SE	*p* ± SE	p_{ent} ± SE	N_{tot} ± SE
Caucagne/St-Léonard	0.76 ± 0.02	0.96 ± 0.02	0.06 ± 0.02	92 ± 0.00
Virets/St-Léonard	0.83 ± 0.05	0.82 ± 0.09	0.10 ± 0.07	16 ± 0.00
L'Ormy/Lens	0.74 ± 0.09	1.00 ± 0.00	0.17 ± 0.10	12 ± 0.00
Sous l'Ormy/Lens	0.70 ± 0.08	0.89 ± 0.08	0.13 ± 0.07	23 ± 0.00

FIGURE CAPTIONS

Fig. 1 Pollard indices for the 38 surveyed plantations.

Fig. 2 Frequency of dispersal events in relation to distance; sexes are presented separately.

Figures

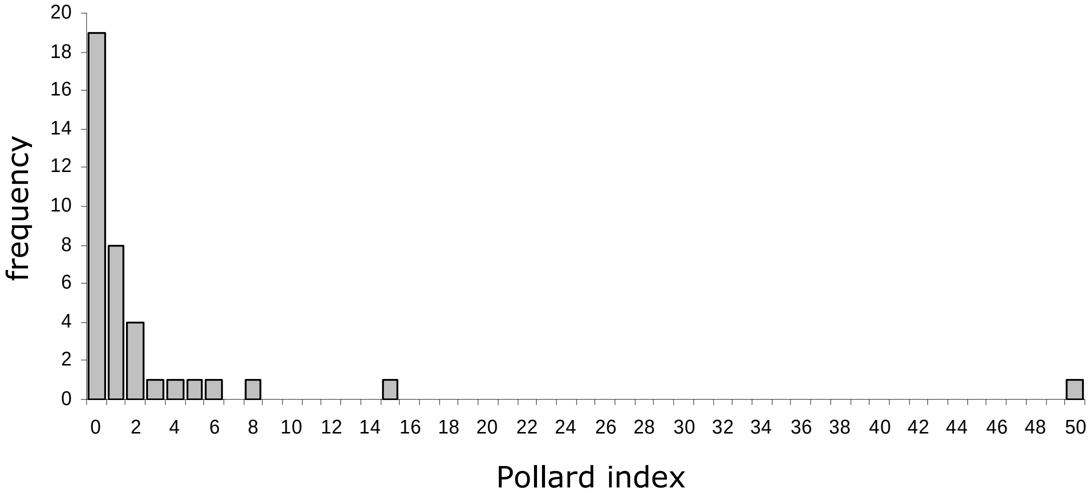
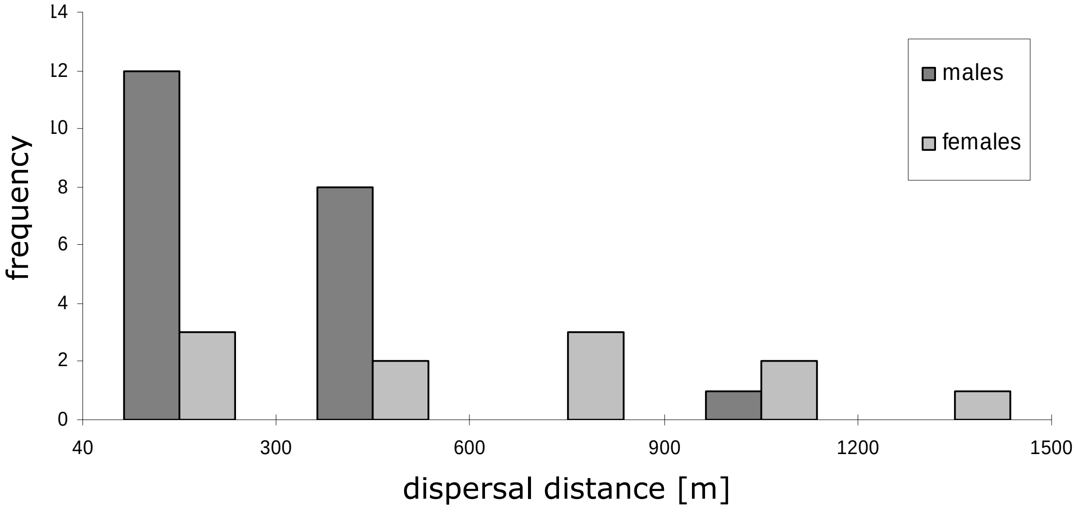


Fig. 1



14
12
10
8
6
4
2
0
frequency
males
females
40
300
600
900
1200
1500
dispersal distance [m]

Fig. 2

Appendix

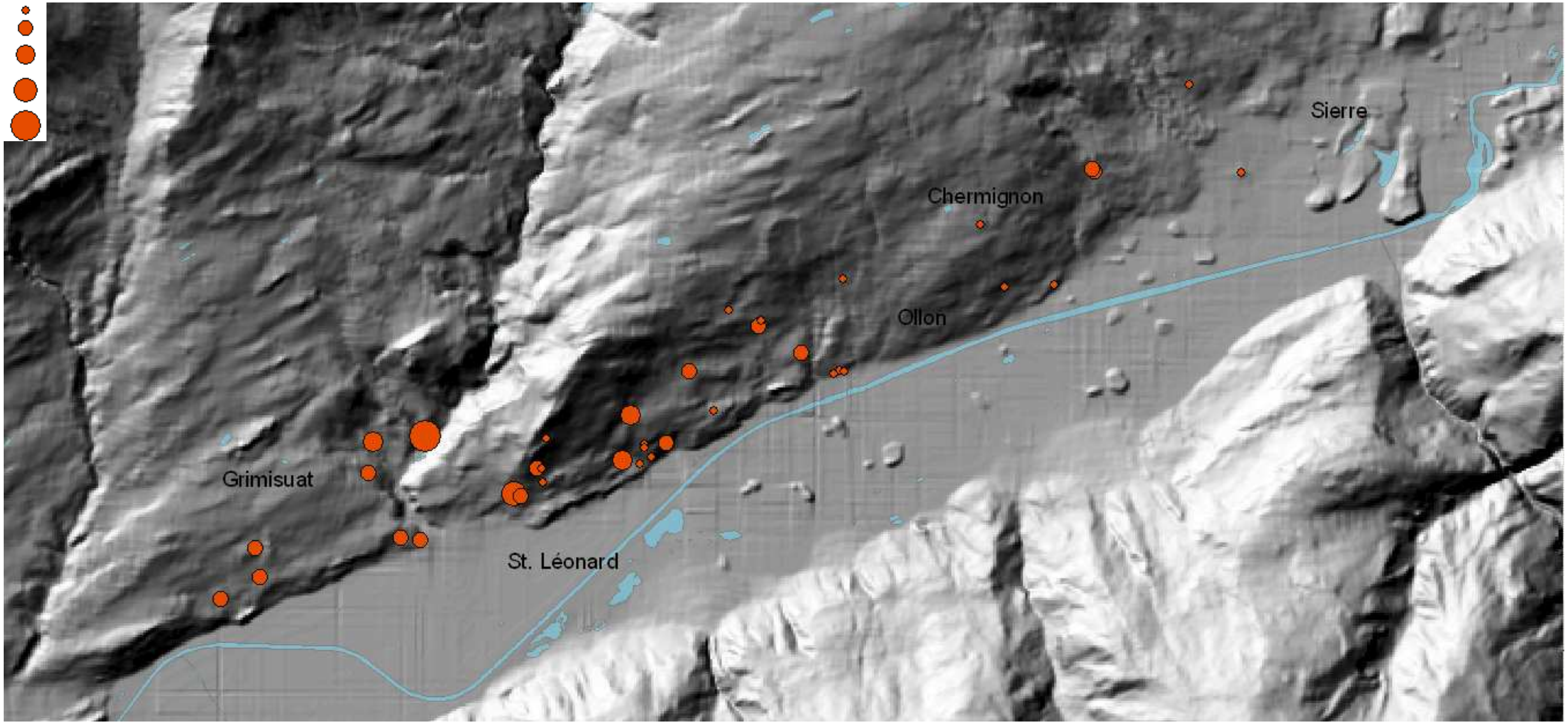


Fig. S1: Location of the 38 plantations around St. Léonard. The size of the dots represents the Pollard index of the corresponding plantation. With increasing size they equate to the following Pollard indices: 0, 1 – 5, 6 – 10, 15, 50.

E r k l ä r u n g

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Bachelor ☐ Master ☐ Dissertation ☐

Titel der Arbeit: Conservation ecology of the endangered Iolas blue *Iolana iolas* (Lepidoptera, Lycaenidae): enhancing monitoring schemes and habitat restoration

LeiterIn der Arbeit: Prof. Dr. Raphaël Arlettaz, Dr. Jérôme Pellet, Antoine Sierro

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

Ort/Datum

Unterschrift