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Evidence-based assessment of butterfly habitat restoration to enhance management practices

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Abstract The decline in distribution and abundance of biodiversity requires evidence-based guidelines for cost-effective conservation management and systematic quantitative assessments of its effects. We investigated the efficiency of a habitat restoration programme aimed at reducing the risk of extinction of the Iolas blue *Iolana iolas* (Ochsenheimer, 1816), one of the rarest butterflies of Central Europe. Using occupancy and capture-mark-recapture (CMR) models accounting for probability of detection, we assessed habitat patch occupancy, habitat selection, demography and dispersal with the aim of testing and refining restoration measures. Count surveys performed at 38 plantations dedicated to the species' unique host plant 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, habitat patch connectivity, and solar radiation. CMR surveys yielded very high catchability (82 %), individual detectability (86 %) rates and limited dispersal capacity. These results form the basis for future efficient count surveys to assess species distribution and abundance. They also provide evidence-based recommendations for improving ongoing habitat restoration: (i) the attractiveness of host plant plantations must be enhanced by promoting mass

In memory of Gilles Carron (1970–2009) who initiated the Iolas blue conservation project in Switzerland.

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blossoming, which can be achieved through systematic autumn pruning of the extant plantations; (ii) new plantations should be created in order to fill in the gaps in the landscape matrix, to increase meta-population capacity through improved habitat connectivity. Finally, this study demonstrates the relevance of efficiency tests as an integral, adaptive phase of any conservation research activity.

Keywords Conservation action plan · Cost-effective conservation · Ecological restoration · Habitat selection · Implementation · Integrated conservation biology

Introduction

The protection and management of semi-natural areas is crucial in preventing biodiversity erosion in human-used ecosystems. However, semi-natural habitats worthy of conservation concern are often heavily damaged and strongly fragmented, calling for biodiversity management measures operating beyond simply setting aside land as nature preserves (Naughton-Treves et al. 2005; Sinclair et al. 1995). Ecological restoration is often necessary to assist in the recovery of a threatened population (Schaub et al. 2009; Schultz and Crone 2005; Sinclair et al. 1995), and this requires a detailed knowledge of its ecological requirements (Hirzel et al. 2004; New 2007; Settele and Kühn 2009). Although many biodiversity restoration programmes have been developed, quantitative appraisals of their success is typically lacking (Pullin and Knight 2009; Schaub et al. 2009). Limited financial resources available for conservation in practice may explain this situation, with investments focusing primarily on project implementation, while omitting tests of efficiency. Quantitative appraisals should, however, be regarded as an integral task of the biological conservation process (Arlettaz et al. 2010). Their absence has recently been recognized as a real caveat in conservation biology, hampering refinements of restoration measures, and the spread of good conservation practice (Memmott et al. 2010).

As is the case for many other plant and animal taxa, butterflies of semi-natural habitats face very high extinction risks, principally due to changes in land-use and management practices that lead to habitat degradation and fragmentation (Robinson and Sutherland 2002; Thomas and Morris 1994; Thomas et al. 2004). Butterflies are frequently used as surrogates when assessing trends in biodiversity and have been the subjects of several habitat restoration programmes, especially in farmland (Kéry and Plattner 2007; Thomas 2005; Van Swaay et al. 2006).

An ecological restoration project of a rare butterfly species threatened with extinction in Switzerland was started in 2000 (Sierro 2007). During the past decades, the Iolas blue underwent a continuous population decline in its last area, in Valais (Carron and Praz 1999). The expansion of vineyards and encroachment of human settlements were identified as the main causes for its rarefaction (Sierro 2007). In order to enhance habitat quality for the butterfly, seedlings of bladder senna *Colutea arborescens* (Linnaeus), its unique host plant in Switzerland, were planted at numerous locations, mostly within vineyards (Sierro 2007).

The goal of this study was to evaluate the efficiency of the habitat restoration measures implemented so that we could propose a set of adjusted evidence-based recommendations with a view to further improving the restoration programme. We first studied habitat requirements of the Iolas blue in order 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. Secondly, we performed capture-mark-recapture (CMR) experiments at four sites to acquire basic information about absolute population sizes and demographic rates (Lande 1988) that enabled us 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 (MacKenzie and Royle 2005). This information is crucial in constructing efficient future monitoring schemes (MacKenzie et al. 2003; Pellet 2008; Pollock et al. 2002). Failing to account for imperfect detectability would otherwise inevitably lead to biases in population abundance, site occupancy and habitat quality models (MacKenzie and Royle 2005). Finally, we analysed the dispersal capacity of the Iolas blue to assess both the extinction risk of the regional meta-population and its ability to re-colonise isolated habitat patches that had been previously deserted (Hanski 1999). This quantitative appraisal of a butterfly restoration programme demonstrates how the new knowledge acquired from tests of efficiency can lead to decisive refinements of monitoring and restoration schemes (Arlettaz et al. 2010).

Materials and methods

Study species

The Iolas blue (Ochsenheimer 1816), belonging to the family of Lycaenidae, 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 and 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 and 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 and 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 and Martín 1993; Tolman and 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 and Wagner 2001). The shrub is native in and around the Mediterranean basin (De Andres et al. 1999) and inhabits the warmest and driest hillsides up to 1,000 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 and Lewington 2008). Iolas blue hibernates as a pupae underneath a stone (Benz et al. 1987; Tolman and Lewington 2008). If Myrmecophily like suspected by Tolman and Lewington (2008) exists, is discussed controversial regarding that it could not be demonstrated so far (Gil-T. 2004).

Study area

The present study was conducted 2010 in Valais (southwestern Switzerland, 46.3°N, 7.3°E). All 38 bladder senna planting sites that were surveyed were located along the southerly-exposed hillside of the Rhône valley between 500 and 950 m altitude, spreading

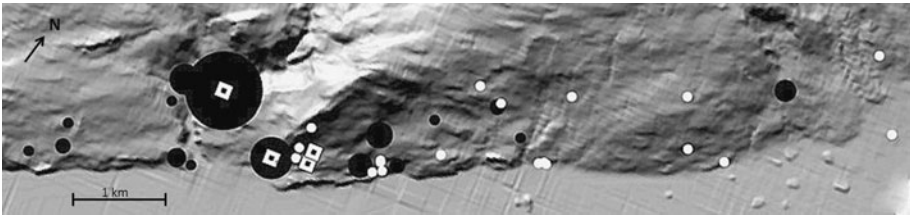

Fig. 1 Map of the study area. The size of the *black discs* is proportional to the amount of Iolas blue observed during count surveys at the specific site. *White discs* represent sites where no Iolas blue where observed. *White squares* represent sites where CMR was carried out

over an area of approximately 10 km^2 (Fig. 1). Within this area two natural *C. arborescens* patches area known to harbour *I. iolas* frequently. Further small patches of *C. arborescens* are spread over the area but are only hardly visited by *I. iolas* (Sierro, pers. comm.).

Restoration program

Between 2000 and 2006, batches of 1–12 bladder senna seedlings collected from local shrubs in mid-November were planted over 38 sites. In the first year after plantation the seedlings were watered 2–3 times during dry periods (Sierro 2007).

The choice of plantation sites was based upon three criteria. Landowners who permitted the plantation had to be found. Plantations were, whenever possible, situated close to locations where the Iolas blue had been detected during former surveys (Carron and Praz 1999). The site had to seem suitable for bladder senna and Iolas blue (exposure to sunlight, southerly-exposed, without competing plants) (Sierro 2007).

Sampling design

Count surveys

Count surveys applying the Pollard index method (Pollard 1977) were performed during the whole duration of the flight season to determine site occupancy rate and relative population abundance. 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 (Pollard 1977)]. On average, each count lasted 10 min during which the number of Iolas blue observed within a 5 m radius around the plantation patch was recorded.

Habitat analysis

We selected 10 habitat variables (Table 1) believed to influence at least one of the Iolas blue's life history stages and to carry some predictive power concerning their relative abundance. We mainly focused on variables representing high management potential; however, other intangible variables were also included. Variables were measured either in situ in the field or via ArcGIS (Environmental Systems Research Institute, California). Given the occurrence of the Iolas blue up to approximately 1,000 m a. s. l. in the study area, we tested for an effect of plantation altitude (Sierro 2007). Altough the potential myrmecophily suggested by Tolman and Lewington (2008) was never proved so far (Gil-T. 2004), we tested the influence of the abundance of *Tapinoma erraticum* (Latreille 1798)

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
Connectivity	$S_i = \Sigma\, p_j \exp(-d_{ij})$ (Hanski 1994)	3.3 ± 1.5	0	5
Bare ground cover	Percent area of non-vegetated ground within 3 m radius around a bladder senna	44.2 ± 23.5	5	95
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
Stone wall	Presence/absence of a stone wall within 3 m radius around a bladder senna	–	–	–
Ant abundance	Number of traps out of 20 per plantation containing *Tapinoma erraticum*	4.1 ± 4.4	0	16
Blossom intensity	Sum of weekly counts of the absolute number of bladder senna flowers in a plantation	3,262 ± 5,110	21	28,545
Bladder senna seedlings	Number of bladder senna shrubs younger than the plantation itself within 5 m radius around a bladder senna bush (Vittoz and 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

in each plantation. Twenty 2 ml Eppendorf tubes, filled with cotton immersed in sugared water, 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.

A combination of habitat patch area and connectivity has been demonstrated to be a good proxy of site-occupancy for butterflies in general (Pellet et al. 2007; Thomas et al. 1992; Wahlberg et al. 1996). In the present study, we determined the number of bladder sennas taller than >1 m because only larger bladder sennas are thought to be attractive for the Iolas blue (Carron and Praz 1999) and used this number as a surrogate for patch area. Because many studies stress the importance of habitat quality and resource availability (e.g. Dennis and Eales 1997; Dennis and Eales 1999; Dennis et al. 2006; Fleishman et al. 2002; Thomas et al. 2001), we estimated the number of flowers on each bladder senna within a given plantation (hereafter referred to as "blossom intensity") on a weekly basis during the whole flight season. Furthermore, blossom intensity highly correlates ($r = 0.95$) with fruit number and therefore also reflects the quantity of resources available to caterpillars (Rabasa et al. 2007, own unpublished information). The occurrence of a stone wall, and the visual estimates for stone and bare ground cover, all considered as positively influencing the the pupation process and herewith the presence of the Iolas blue (Carron and Praz 1999; Tolman and Lewington 2008), were noted within a 3 m radius of each bladder senna, this being the maximum expected distance caterpillars might cover. Values for stone and bare ground cover were averaged for each site, whereas the occurrence of a stone wall was taken into account, if at least part of it was closer than 3 m to any bladder senna. The number of bladder senna seedlings was also counted within a 5 m radius (99 % of dispersal range of seeds (Vittoz and Engler 2007)) around each plant to test for converging habitat preferences in the plant host and the butterfly, and to assess the degree of 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. Solar radiation calculations were based on the digital elevation model using the algorithm of Fu and Rich (2002), as implemented in the tool Solar Radiation Analysis in ArcGIS 9.3 (Esri 2009).

Characteristics for monitoring

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) that had harboured large population sizes over the past years. CMR experiments were conducted under the same weather conditions as count surveys. During 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. In 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 took 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).

Additionally an analysis was performed to obtain estimates of the Iolas blue's dispersal ability. The analysis included all Iolas blue from the CMR experiments, in addition to those that had been haphazardly hand-netted on any other occasion in the field. All the captures and recaptures were localized using GPS, 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 12 models, including 10 defined a priori, as well as the full model and the intercept model (Table 2 and supplementary information).

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 12 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. We used an information theoretic approach for model classification. Models were ranked by their decreasing AIC_C (Burnham and Anderson 2004; Johnson and Omland 2004). Models with $\Delta AIC_C \leq 2$ were considered to have substantial support (Burnham and Anderson 2004). In addition, AIC_C weights ($wAIC_C$), which indicate the relative support of a model (Burnham and Anderson 2002), and pseudo-R^2 (Veall and Zimmermann 1996), were calculated for each model.

Table 2 Selection of candidate models for Iolas blue abundance. Models are ordered by decreasing AIC_C

#	Model	*K*	AIC_C	ΔAIC_C	$wAIC_C$	Pseudo-R^2 (%)
6	*N*(connectivity + bloom + seedlings + solrad) *p*(.)	5	124.635	0.000	0.206	83.3
5	*N*(connectivity + bloom) *p*(.)	3	127.296	2.661	0.180	81.0
4	*N*(connectivity + bloom + senna.quantity) *p*(.)	4	129.722	5.087	0.160	81.1
8	*N*(ant + bloom + stone) *p*(.)	4	130.142	5.507	0.156	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	87.3
7	*N*(bloom + seedlings + senna.quantity + solrad) *p*(.)	5	142.185	17.550	0.086	78.3
11	*N*(altitude + connectivity + senna.quantity) *p*(.)	4	161.632	36.997	0.032	72.0
3	*N*(connectivity + senna.quantity) *p*(.)	3	197.996	73.361	0.005	60.9
9	*N*(ant + stone.wall + bare.ground + stone) *p*(.)	5	210.325	85.690	0.003	58.8
12	*N*(altitude + connectivity + solrad) *p*(.)	4	248.352	123.717	0.000	47.2
10	*N*(stone.wall + bare.ground + seedlings + stone) *p*(.)	5	275.435	150.800	0.000	40.2
1	*N*(.) *p*(.)	1	406.751	282.116	0.000	0.0

The sample size (n) is 38 for all models, K is the number of parameters

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

Characteristics for monitoring

CMR data was analysed using the POPAN formulation of the Jolly-Seber approach in software MARK 6.0 (Veall and Zimmermann 1996; White and Burnham 1999). CMR data of all four sites were analysed separately to calculate the catchability (p). Estimates of the apparent daily survival were used to calculate the life expectancy ($l = -1/\ln(\Phi)$) (Mallet and 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 (Pellet et al. 2012).

Dispersal rate was defined as the proportion of individuals recaptured at a different patch then the one on which they were initially marked. Patches were defined as separate, if their boundaries were at least 40 apart (Rabasa et al. 2007).

Results

Count surveys

Iolas blue were observed at 19 out of 38 plantations (occupancy 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.

Habitat analysis

The model best explaining Iolas blue's abundance (Table 2) had anAIC_C weight of 0.206. It included connectivity, blossom intensity, and number of seedlings, which are all positively related to abundance, plus variation of solar radiation, the latter having a negative influence. The pseudo-R^2 value for this model is extremely high (83.3 %).

Characteristics for monitoring

Estimates for apparent daily survival (±sem) 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. 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. Total population sizes (N_{tot}) were between 12 and 92 It should be noted that the very small standard errors are a by-product of a very intensive sampling effort in all four populations, and are not due to an artefact. 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).

During the whole flight season 180 Iolas blue were marked and 69 individuals (38 %) were recaptured at least once. From all the observed movements 26 % were considered as dispersal events but most (78 %) dispersal distances were shorter than 550 m, with a maximum distance of 1,490 m.

Discussion

The present study provides evidence for the success of the habitat restoration actions undertaken for the Iolas blue. Four to ten years after being specifically planted for the Iolas blue, half of the bladder senna planting sites were occupied by the targeted butterfly, which demonstrates well a species' ability to colonise newly created habitats rather quickly (Carron and Praz 1999). This success of the undertaken habitat restoration stands in line with the findings of comparable restoration programs (Martilla et al. 1997; Pfitsch and Williams 2009).However, the very low population size estimates (Pollard's index) obtained for 18 of the 19 occupied plantations show that the vast majority of local populations were highly exposed to demographic stochasticity. In order to enhance conservation strategies this situation clearly calls for greater understanding of the underlying meta-population mechanisms.

Habitat suitability models revealed that the abundance of this butterfly is best explained by bladder senna's blossom intensity and the location of these plants within the meta-population landscape. The number of bladder senna seedlings, and amount of solar radiation also influenced Iolas blue's abundance, albeit to a lesser extent. Capture-mark-recapture (CMR) experiments indicated a much shorter life expectancy than anticipated based on species' body size and life history (Beck and Fiedler 2009; Lindzey and Connor 2011; Vandewoestijne et al. 2008). They also revealed very high catchability and individual detectability rates, at least under standardized survey conditions as applied here, reflecting highly territorial focused behaviour. All these results have implications for future population monitoring and habitat improvement that we discuss below.

The mostly very low population size estimates (Pollard's index) were expected due to former field experience but comparable data had never been gathered in this area so far. Iolas blue was always relatively rare in the area but habitat degradation in the former decades had led to a dramatic decline in abundance (Carron and Praz 1999). Hence, our data can be used as a reference point for the necessary upcoming monitoring programs.

Several butterfly studies have best described patterns of patch occupancy using an area-isolation paradigm of meta-population dynamics (Pellet et al. 2007; Thomas et al. 1992; Wahlberg et al. 1996), whereas others simply stressed the importance of habitat quality and resource availability (Dennis and Eales 1997, 1999; Dennis et al. 2006; Fleishman et al. 2002; Thomas et al. 2001). Our analysis focused on abundance of butterflies, as well as including variables expressing both meta-population structure (patch area represented by quantity of senna bladder and connectivity), and habitat quality, and resource abundance (e.g. blossom intensity). Our best-fitted model for species-habitat associations consisted of four predictors describing both connectivity and habitat quality/resources abundance, thus reconciling the two above paradigms of patch occupancy. Connectivity is more likely to influence abundance of Iolas blue 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 (Moilanen and Nieminen 2002). Blossom intensity varied by two orders of magnitude between occupied sites, directly impacting on relative abundance. In effect, *Colutea* flowers are believed to be an almost exclusive nectar source for the adult Iolas blue (Rabasa et al. 2008). Blossom intensity also correlates with the quantity of bladder senna fruits, the latter being the exclusive diet of Iolas blue caterpillars (Rabasa et al. 2007, own unpublished information). We also noticed that high blossom intensity generally correlates with a long flowering season, during which the emergence of flowers and fruits is staggered over time. This guarantees lasting availability of attractive nectar sources and young fruits that may stimulate both oviposition and larval development (Rabasa et al. 2005). The negative influence of solar radiation is intriguing and, at first glance, counter-intuitive given the mostly southern distribution of the Iolas blue. Solar radiation might influence Iolas blue's abundance indirectly. Hot conditions may negatively affect the reproductive performance of bladder senna. Even though this bush occurs extensively in the Mediterranean basin, we were able to observe how rapidly flowering and fruit ripening took place during warm spells in the study area, probably contributing to the reduction of both foraging opportunities for imagos and fruit palatability for larvae. The positive influence of bladder senna seedlings on Iola blue's abundance might 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 thus affect the future reproductive potential of a site.

The abundance of *T. erraticum* wasn't included in the best models. This can be seen as a further hint to the absence of myrmecophily in Iolas blue, as supposed by Gil-T (2004).

There is some controversy about the relevance of CMR studies for biological conservation studies of endangered butterflies. CMR experiments are labour-intensive (Haddad et al. 2008), and marking can damage butterflies (Murphy 1987), thereby compromising the probability of recapture (Singer and Wedlake 1981). This may potentially generate biased population estimates, especially when sample size is small (Haddad et al. 2008). We believe that the relatively large body size of the Iolas blue, combined with few re-netting events limited these impacts when conducted by properly skilled and trained workers. Notwithstanding other drawbacks, we obtained acceptable estimates in all research topics. First, we were able to provide population size estimates for the four presumably largest remaining Iolas blue subpopulations in Switzerland, thereby confirming the species' red list status, and assessing its high susceptibility to demographic stochasticity, i.e. we highlighted the need to improve habitat restoration. The study also established the disproportionate importance of one single species plantation for the survival of the whole meta-population and identified the basic elements for future cost-effective monitoring schemes, although we have to keep in mind that, for butterflies, both within-season, weather-dependent, as well as between-years, population fluctuations may be considerable (Rabasa et al. 2007), whereas our study took place during one year only. Secondly, the average life expectancy of adults was much lower than the initially expected two weeks, but still comparable to the lowest values obtained on 24 species of Lycanidae (Beck and Fiedler 2009; Meyer-Hozak 2000; Thomas et al. 2010). Given the short life expectancy and the fact that each individual should be available for capture 3–4 times to allow powerful CMR modelling (Pellet and Gander 2009), we suggest future CMR experiments be repeated daily or every second day, under suitable weather conditions. Thirdly, catchability (0.82–1) and individual detectability (0.86) were very high, as a result of a large body size, conspicuous colour and typical male patrolling behaviour. Habitat openness (vineyards) and surveys restricted to warm and sunny days 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. We thus advocate a hybrid approach for future monitoring schemes, combining short-term local CMR experiments with frequent count surveys of all habitat sites according to the protocol used here.

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 a few individuals flying long distances (maxima of 1,490 and 1,792 m, in this study and Rabasa et al. (2007), respectively), is commonly observed in butterflies (Brommer and Fred 1999; Gutiérrez et al. 1999; Wahlberg et al. 2002). 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.

Conclusions

The ecological restoration program launched in 2000 was instrumental in securing medium-term viability of the last Iolas blue population of Switzerland. More concerted efforts are now needed to guarantee its long-term persistence. We present a conservation roadmap based on our current knowledge of the species' ecology and on results obtained through quantitative assessments of implemented restoration measures. The core population, harbouring almost 50 % of the entire surveyed meta-population, probably functions as a source population (Pulliam 1988), with all other groups appearing to be extremely vulnerable. It is therefore urgent to protect this population and to gain new source populations via more appropriate management and more efficient habitat restoration action. A first series of improved management measures would consist in increasing blossom intensity in all plantation patches. Limiting herbicide application in marginal bushy areas around vineyards would be a major obvious contribution. Regular pruning outside the vegetation period would be another cost-efficient way to promote bladder senna blooms. A second series of measures would be to increase the meta-population capacity of the landscape by increasing habitat connectivity in the vineyard-dominated matrix (Hanski and Ovaskainen 2000). This could be achieved by planting new patches of at least 20 large bladder sennas each within 550 m of an existing population. Plantation sites should be neither too hot nor too dry. We believe 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 and 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 for the last remaining Swiss population of the Iolas blue in an efficient and effective manner. More generally, the study also demonstrates the relevance of quantitatively testing the effectiveness of implemented restoration measures. This phase would greatly benefit from inclusion as an integral, obligatory phase of any conservation action plan (Arlettaz et al. 2010) as it enables management policies to be re-adjusted and the most cost-effective implementation practices to be adopted for the sake of biodiversity preservation.

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