

Drones for butterfly conservation: larval habitat assessment with an unmanned aerial vehicle

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Received: 11 December 2015 / Accepted: 24 June 2016
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Abstract

Context Evidence-based nature conservation focuses on ecological facts and the incorporation of knowledge on the ecology of species, including its entire life cycle. In butterflies, imagos and its larvae often demand specific and diverging micro-habitat structures and resources. In consequence, ecological requirements of the imaginal and pre-imaginal stage have to be taken into consideration to conduct effective conservation management.

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-016-0409-3](https://doi.org/10.1007/s10980-016-0409-3)) contains supplementary material, which is available to authorized users.

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Objective Here we analyse ecological pre-requisites of imagos and larvae for two lycaenid butterfly species, the common blue *Polyommatus icarus* and the adonis blue *Polyommatus bellargus*. Both butterfly species occur in calcareous grasslands and mainly depend on two plant species at our study site, the horseshoe vetch *Hippocrepis comosa* and bird's-foot trefoil *Lotus corniculatus*. These plant species serve as nectar sources and larval host plants for the two butterfly species.

Methods First, we assessed the occurrence of imagoes and larvae of the two butterfly species and recorded various micro-habitat characteristics, like the number of flower buds of the two main host plants, the surrounding vegetation height, percentage of bare soil, availability of shadow, and the distance to and geographic direction of thickets at respective sites. In a second step we took high resolution aerial pictures from our study area using an unmanned aerial vehicle (drone). Based on these aerial pictures and the information on the larva's habitat preference from our field observations, we trained a habitat suitability model to identify micro-habitat structures suitable for larvae of the two butterfly species.

Results We found that abundance of imagos is positively correlated with flower bud density of the two host plants. Low vegetation height and high proportion of bare soil (but not flower bud density) positively influence egg oviposition. The calculated habitat suitability models predict the occurrence of high quality larval habitats with high prediction power (AUC = 0.72).

Conclusions This combined data set consisting of field observations, high resolution aerial pictures taken from an unmanned aerial vehicle, and models underline that (1) species with complex life cycles may request more than one habitat niche, depending its stage of development, and (2) high resolution aerial pictures taken from drones provide valuable background data to generate habitat suitability models—even on a micro scale but covering larger parts of a landscape.

Keywords Aerial picture · Drone · Evidence based nature conservation · Habitat suitability model · Host plant · Imaginal stage · Larval ecology · Micro-habitat structures · Pre-imaginal stage

Introduction

Knowledge on the ecology of species is the prerequisite to improve species conservation management (Sutherland et al. 2004). Here, information covering the entire life cycle of organisms has to be taken into consideration, particularly for species demanding more than one habitat resource like multiple micro-habitat niches within one ecosystem depending the stage of its life cycle. Amphibians for example need an aquatic and terrestrial habitat, both reachable. Thus, amphibians suffer extremely under ongoing habitat destruction and a split between both habitat types (the habitat split debate, see Becker et al. 2007; Quesnelle et al. 2015; Soininen et al. 2015).

Arthropods frequently request more than one micro-habitat niche during their life cycle, mostly located within one ecosystem (e.g. the pre-imaginal vs. imaginal habitat in butterflies). Imagines of butterfly species often need specific flowering plant species as nectar source; in parallel, the same taxon might be highly dependent on one or some few specific larval host plants (Bink 1992). In addition to the presence of the respective plant species, the performance of a micro-habitat might strongly affect the attractiveness for the butterfly species (Rausher 1979; Dennis et al. 2006; Dolek 2006; Fartmann 2006; Bräu et al. 2010). Various studies underline that specific micro-habitat structures are the pre-requisite for successful egg oviposition and larval development, as indicated for a number of butterfly species (Fartmann 2006).

Prominent examples provide representatives of the butterfly genus *Phengaris*: these myrmecophilous butterfly species strongly depend on one specific larval host plant and one (or few) specific host ant species for successful development (Thomas et al. 2011). Only marginal modifications in the micro-habitat structures may change the abundance of host plant and host ant species which might have detrimental effects on local butterfly populations (Thomas et al. 2011).

Various studies underline the relevance of micro-habitat conditions for butterflies (Fartmann and Hermann 2006; García-Barros and Fartmann 2009). Apart from the presence of a specific larval host plant, micro-habitat structures are of high relevance for successful egg oviposition by female butterflies. For example, host plants outstanding the surrounding vegetation cover or solitary host plant individuals as well as host plants located at the edge compared to inside the host plant occurrences are preferred for egg oviposition by many butterfly species (Fartmann and Hermann 2006). Further studies underline that micro-climatic conditions (related to exposition and inclination) affect the duration of larval development and thus contribute to the quality of a larval habitat (Dolek and Geyer 2000; Dolek 2006). In addition, local predation, parasitoid pressure and inter- and intraspecific competition may affect the quality of a larval habitat (Hafner 2006). In consequence, various factors are of relevance to convert a “potential” habitat into a “preferred” habitat, according the species’ needs.

Until today, all larval ecology analyses were performed by classical aut-ecological field observations, and thus were spatially restricted to local sites (see Fartmann and Hermann 2006, with references therein). Unmanned aerial vehicles equipped with high resolution cameras may provide suitable information about micro-habitat structures, assessed for even larger areas. Currently, drones became prominent in applied and theoretical (scientific) conservation biology (Anderson and Gaston 2013; Chabot and Bird 2013; Schiffman 2014). Improved mechanic flight systems with new multispectral high resolution cameras has led to an increase of the application of unmanned aerial vehicles for land cover (change) detection and biodiversity assessments (Wich and Koh 2012; Luo et al. 2014; Arts et al. 2015; Chabot and Bird 2015; Maffey et al. 2015).

In this study we quantify effects from micro-habitat structures on the occurrence of imagines and larvae for

two closely related lycaenid butterfly species, the common blue *Polyommatus icarus* and the adonis blue *Polyommatus bellargus*. Analyses were performed at a calcareous grassland site close to Freising, Germany. Both target butterfly species mainly depend on two nectar and larval host plant species, the horseshoe vetch *Hippocrepis comosa* and birds-foot trefoil *Lotus corniculatus* (Reinhardt et al. 2009). We combine detailed field assessment of small scale micro-habitat characteristics with micro-scale habitat suitability models based on high resolution aerial pictures taken from an unmanned aerial vehicle (drone). Models were trained using our field observations on the spatial distribution of host plants occupied and unoccupied by larvae. Based on this integrative approach we raise the following questions:

1. Does flower bud density of the two host plants affect the presence of imagines and larvae of the two butterfly species?
2. Do micro-habitat structures affect egg oviposition and subsequently the quality of the larval habitat?
3. Do high resolution aerial pictures taken from a drone provide information to predict suitable larval habitats of butterflies?

Materials and methods

Study site

The Dietersheimer Brenne was selected as study site. This calcareous grassland is located south of Freising, close to the Isar river (48.29°N, 11.68°E). This study area covered 3.84 ha with 826 mm precipitation per year (mean over the past 20 years) and 8.7 °C average temperature (according to the closest local weather station, Freising, Germany). It is characterised by extreme solar radiation, high temperature peaks, dry climatic conditions as well as nutrient deficiency (Autengruber et al. 2007). Dominating vegetation formation creates the Mesobromion, characterised by sparse vegetation and spots of bare soil. The Mesobromion consists of a species rich flora and fauna, including many rare and protected taxa (Habel et al. 2013). The study site is bordered by forests and intensively used agricultural land. Current conservation management strategies preserve the open character of this vegetation type.

Model species

As study species we selected two typical calcareous grassland lycaenid butterflies, the common blue *Polyommatus icarus* and adonis blue *P. bellargus*. The species' distributions of both butterflies cover the entire Western Palaearctic region, including the British Isles (Tolman and Lewington 1997). Imagines are on the wing from end of May until September, in two to three generations. Its main nectar sources and larval host plants are the horseshoe vetch *H. comosa* and birds-foot trefoil *L. corniculatus* (Reinhardt et al. 2009). Agricultural intensification and subsequent destruction of extensively cultivated (calcareous) grasslands and the fragmentation of the remaining habitat patches caused a severe decline of both butterfly species during the past decades (Reinhardt et al. 2009). Thus *P. bellargus* is listed as vulnerable on the Red List of Bavaria (LfU 2015), and classified as vulnerable according to the German Red List (Bolz and Geyer 2003).

The butterflies' host plant species, *H. comosa* and *L. corniculatus* are common along road verges and shrubs, forest edges, in extensively used meadows and calcareous grasslands, but can also be found in nutrient rich pastures. These plant species are flowering mainly during May and June (but at some localities until September, Reinhardt et al. 2009).

Data collection

We assessed the exact location of the two food plants *H. comosa* and *L. corniculatus* with the GPS device Garmin etrex 10 and counted the number of flower buds for each plant individual found over our study site during June 2015. We assessed the occurrence of imagines of *P. icarus* and *P. bellargus* (including males and females) along fixed line-transects throughout our study site, covering the entire area during June 2015. In total we set 20 transects with 150 m length covering the entire study site. Here, the two targeted lycaenid species were counted inside a 5 m buffer at both sides along these transects. This butterfly count was performed six times during noon time in June 2015. The location of each individual observed was captured with a GPS device Garmin etrex 10. For each observation we recorded the respective number of flower buds of the two host plant species within a 4 m² radius around each point where a butterfly could be

observed. To minimize inaccuracies from GPS measurements (Garmin 2016), assessments on the location of flower buds and butterflies were exclusively performed during cloud-free days and by using the waypoint averaging function of the device. All measurements had a CEP₅₀ value of less than 3 m.

Occurrence of the pre-imaginal stage of *P. icarus* and *P. bellargus* was assessed by active search for eggs and species specific feeding traces from caterpillars; the detection of caterpillars itself was difficult as they are mainly active during the night and hidden in the layer of ground litter during the day. Assessments were performed covering our entire study site, during spring and summer 2014 and 2015.

We randomly selected 84 food plants with the ArcGIS function Create Random Points (ESRI 2015). We classified the food plants into occupied and unoccupied by larvae of the two butterfly species and evaluated the level of occupancy according the number of eggs oviposited and signs from larvae (see above). We assessed the following micro-habitat characteristics: flower bud density (flower buds/m²), vegetation height (cm, classified into low ≤ 10 cm, medium 10–30 cm, and high ≥ 30 cm), vegetation density (classified into low 0–33 %, medium 33–66 %, high 66–100 % coverage), availability of bare soil (presence/absence, and classified into low 0–33 %, medium 33–66 %, high 66–100 % coverage), distance to the next shrub (in m, classified into close 0–2 m, medium 2–4 m, far ≥ 4 m distance), and the geographical direction of shrubs (N, S, E, W). Data collection was performed by three people for 10 min at each position. Each study plot had a size of 2 × 2 m.

Statistics

We performed one way ANOVA, one-way and two-way PERMANOVA (Anderson 2001, Bray-Curtis distances) to relate the number of imagos depending flower bud density. Identical one way ANOVAs were performed to relate the number of eggs and the presence/absence of signs from larval feeding of the two butterfly species to the categorical variables as vegetation height (classified into the categories low, medium, high), vegetation density (classified into the categories low, medium, high), bare soil coverage (present, absent), and distance to nearest shrubs (m) (further details on the categories see above). All

raw data are provided in Supplementary Material Appendix S1.

Aerial pictures

Aerial pictures were taken using an unmanned aerial vehicle (DJI Phantom 2) equipped with a H4-3D Zenmuse gimbal and a light-weight digital camera (GoPro HERO 4 Black). The flight was conducted in June 2015 at a height of 40 m using an orthogonal camera attachment with 12MP resolution, 20 mm field of view (FOV) and 2 s time lapse interval while flying with 5 m/s. Flight path was prepared using the photogrammetry tool of DJI Ground Station 4.0 software, with the stop and turn turning mode setting. Mission was prepared with 50 % overlap between consecutive pictures and between neighbouring flight lines to minimize lens distortion effects on results. In total, four flight lines in one mission (15 min) were conducted, with each flight line of 250 m. In total 120 usable pictures were taken during this mission. Single aerial pictures were combined afterwards with AgiSoft Photoscan Professional software using high-quality dense cloud processing and mesh construction settings. Pictures were calibrated using calibration tools within Photoscan software and fisheye camera type to reduce lens distortions. Based on sufficient ground control points processed imagery was exported as orthomosaic in geotif raster file format with 0.02 m cell size for subsequent use in species distribution modelling. Ground control points were placed within the Agisoft Photoscan Professional software with the help of markers and preset accuracy settings of 10 m for marker accuracy. The processed orthomosaic with the georeferenced ground control points reached accuracy values between 0.003 m (for latitudinal errors) and 0.005 m for longitudinal errors.

Aerial pictures were decomposed into RGB channels, which were used as input variables for the habitat suitability models. For both, occupied and unoccupied plant sites we approved all locations again in the field using the previously taken GPS coordinates which are now combined with the generated and georeferenced orthomosaic. As all point localities coincide with our field sites we used all data for further habitat suitability models.

Habitat suitability models

Based on these georeferenced high resolution aerial pictures, and the assessed parameters on the micro-habitat structures around occupied and un-occupied *H. comosa* and *L. corniculatus* plant positions we calculated a nested set of habitat suitability models (HSMs), first based on all host plants assessed, and second based on host plants which were occupied by the butterflies larvae (and showing specific micro-habitat structures, see results).

HSM for feeding plants—An ensemble species distribution model (SDM) was computed using the *biomod2* framework for Cran R (Thuiller et al. 2013) based on single SDMs computed using four different algorithms (GAM, GBM, GLM, and Maxent). Two sets of each 1000 pseudo-absence records were randomly selected within an area enclosed by circular buffers of 50 m around the species records. In total 415 unique GPS coordinates of feeding plants within the area covered by the aerial pictures were available, which were six times randomly split into 80 % used for model training and 20 % used for evaluation resulting in 24 single SDMs (2 sets of pseudo-absences * 3 evaluation runs * 4 algorithms). Accuracy of SDMs was assessed using the Area Under the Receiver Operating Characteristic Curve, AUC (Swets 1988) as well as the point biserial correlation coefficient (COR) computed using the *dismo* package for Cran R (Hijmans et al. 2015). Subsequently, a weighted ensemble HSM was computed based on all single HSMs with AUC scores >0.7 using a decay factor of 1.6. As non-fixed presence-absence threshold as recommended by Liu et al. (2005) we skipped 10 % of the records with the lowest probability scores in the ensemble HSM assuming that 10 % of the species records are outside of potential habitat patches due to georeferencing accuracy. In the final model only suitable habitat patches with a minimum size of 10×10 cm were retained as these are likely to provide sufficient nutrition for the larvae.

HSM for feeding plants occupied by larvae—Within the area predicted to be suitable for food plants according to the ensemble SDM 28 unique GPS coordinates of feeding plants occupied by larvae were available. As most algorithms available within the *biomod2* framework require higher numbers of species records for reliable performances (Wisiz et al.

2008), we chose Maxent 3.3.3.k (Phillips et al. 2006) as only algorithm herein as it is relatively insensitive to low numbers or records. The training area of the HSM was restricted to those parts of the study area which were suggested to be suitable for the feeding plants according to the ensemble to develop a model discriminating between preferred reproduction sites by butterflies and the general potential distribution of feeding plants. Splitting the larvae records 100 times into 80 % used for model training and 20 % used for model evaluation a final consensus SDM was computed as average across all single SDMs. As presence-absence threshold we used the minimum score at the larvae records. Accuracy of SDMs was again assessed using AUC (Swets 1988) as well as the point biserial correlation coefficient computed using the *dismo* package for Cran R (Hijmans et al. 2015).

Results

In total we recorded 645 flower buds of the two host plant species, *H. comosa* and *L. corniculatus* in 2015 over our study area. We observed 133 imagos of *P. icarus* and *P. bellargus* (taxa combined) at 61 locations, spread over the grassland area (ranging from 1 to 4 individuals per site and date of observation). 63 of the 84 assessed larval food plant locations were occupied by larvae from at least one of the two butterfly species. Number of eggs ranged from 0 to 8 eggs/m², with a mean value of 1.1 eggs/m² (calculated exclusively for occupied sites). An overview of the raw-data is given in Supplementary Material Appendix S1.

The number of butterfly imagos observed increased significantly with flower bud density assessed for the 4 m² circle around each imago observed ($R^2 = 0.76$, $P < 0.001$). The number of deposited eggs significantly decreased with increasing vegetation height and vegetation density (Tables 1, 2; Fig. 1). Both species preferred plants surrounded by low vegetation height and high percentage of bare soil over those of dense vegetation for egg oviposition (Table 1). Vegetation density was highly positively related to vegetation height (ANOVA: $F(2,80) = 27.6$, $P < 0.001$). Egg densities did neither depend on the density of host flower buds (Fig. 1b), nor on the distance to the nearest shrub (Fig. 1c).

Table 1 A contingency table for egg oviposition (based on counted eggs and characteristic feeding signs from the target butterflies) at different vegetation density and presence of bare soil (presence/absence) identified for eggs preference for thin

Soil/vegetation	Eggs			Larvae		
	Low	Medium	High	Low	Medium	High
Yes	63	13	0	12	11	1
No	8	13	1	2	8	18

vegetation in combination with a high proportion of bare soil ($\chi^2 = 19.9$, $P < 0.001$) and for larvae preferences for either dense vegetation without upper soil or for dense vegetation on upper soil layer ($\chi^2 = 22.6$, $P < 0.001$)

Table 2 Two-way PERMANOVA identified the presence of bare soil and vegetation density as being significant triggers of egg numbers of *Polyommatus icarus* and *P. bellargus*

Factor	Eggs		Larvae	
	df	F	df	F
Soil	1	15.9***	1	1.7
Vegetation height	2	19.0***	2	0.6
Interaction	2	<0.01	2	<0.01
Residual	26		78	
Total	31		83	

Habitat suitability models (HSMs) matched well with our field observations (Fig. 2a–c), wherein warmer colors indicate areas of high habitat suitability, i.e. localities with the respective larval habitat and micro-habitat structures (low vegetation height and density, high proportion of bare soil). Verification in the field approved these predicted sites.

HSM feeding plants

In the ensemble HSM for the feeding plants of both butterfly species RBG band 3 had the highest overall contribution (40.6 %), followed by band 1 (35.8 %) and band 2 (23.6 %). The general discrimination ability of the HSM between suitable habitats for feeding plants and surrounding vegetation was high (AUC = 0.72, COR = 0.39). However, the discrimination ability of this HSM between plants with larvae and random background habitats was lower (AUC = 0.66, COR = 0.141). Comparing the performance of the four different algorithms discrimination abilities were very similar on average (AUC_{GAM} = 0.72; AUC_{GBM} = 0.72; AUC_{GLM} = 0.72; AUC_{Maxent} = 0.71).

HSM for larvae

In the HSM for the occurrence of larvae of both butterfly species the probability of occurrence of

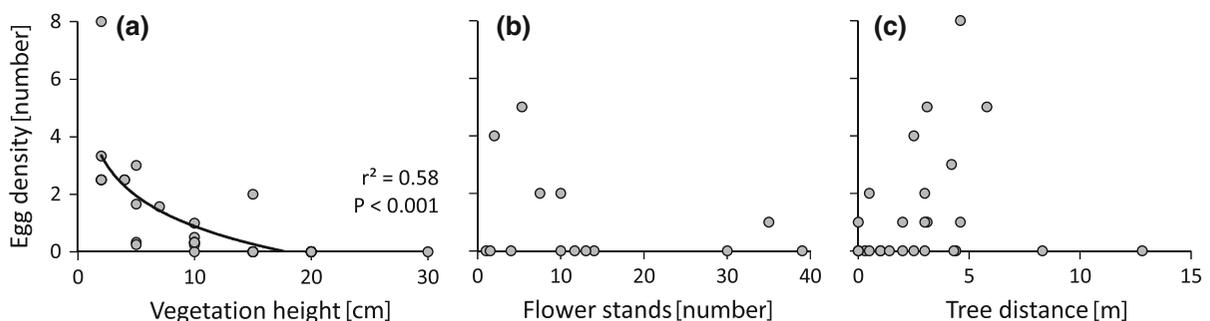
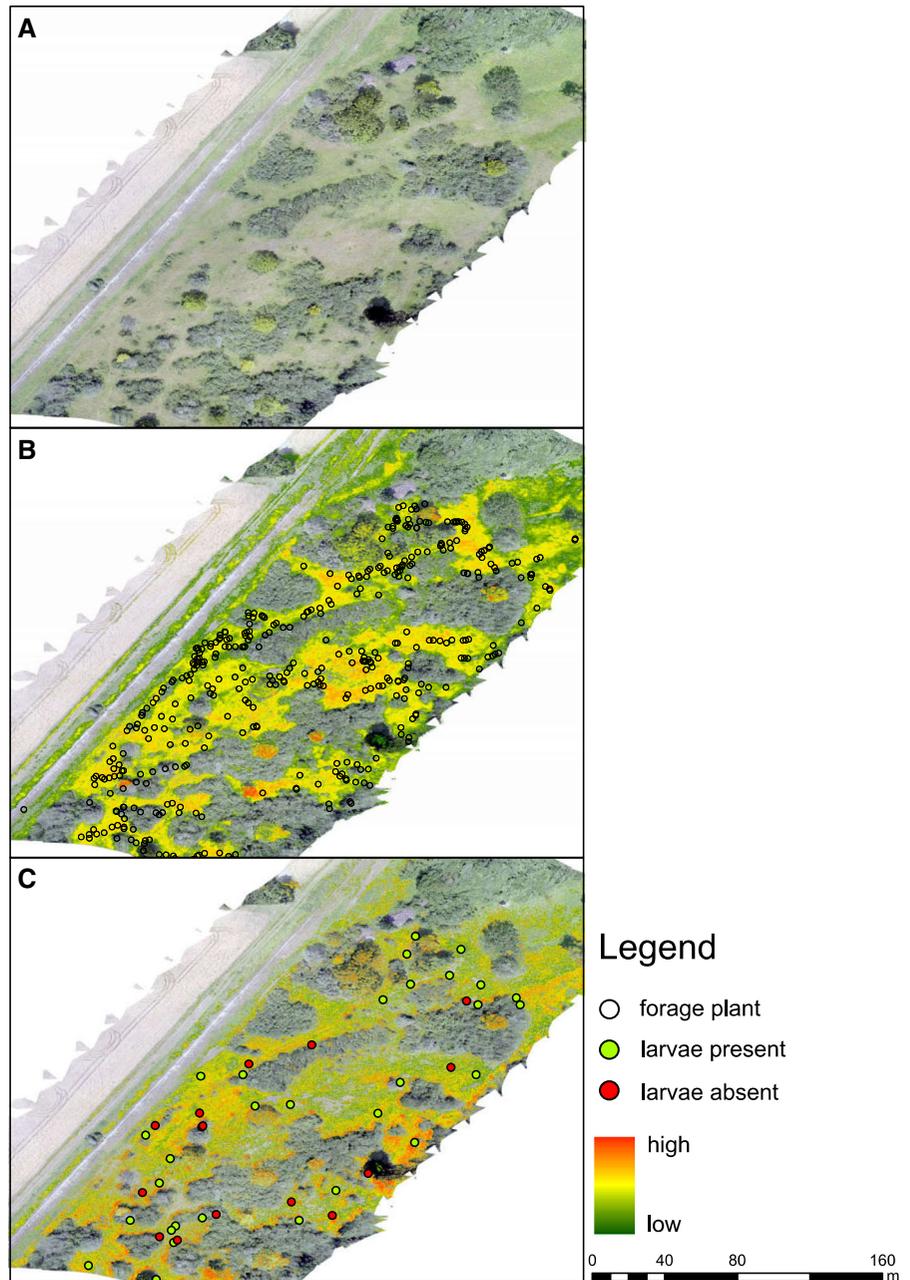


Fig. 1 Combined egg density of *Polyommatus icarus* and *P. bellargus* decreased with vegetation height (cm) (OLS, parametric $P < 0.001$) (a), but was independent of the density of

host flower buds (b), and the distance to closest shrubs (c) even when eliminating two outliers ($P > 0.05$)

Fig. 2 Transformation of a high resolution aerial picture (a) into habitat suitability model for larval habitats of the two lycaenid butterflies *P. icarus* and *P. bellargus*, based on the occurrence of the two main host plant species (b), and on larval host plant occurrences occupied by larvae (c)



feeding plants (ensemble HSM) had the highest contribution (67.2 %), followed by RGB band 3 (22.6 %), band 2 (7.6 %) and band 1 (2.6 %). The general discrimination ability of the HSM between random background and actual occurrence of larvae was higher compared to the ensemble HSM (AUC = 0.72, COR = 0.22).

Discussion

Imaginal and pre-imaginal habitat

The spatial distribution of the two main nectar and larval host plant species *L. corniculatus* and *H. comosa*, and the occurrence of imagines and larvae

showed that the butterfly stage becomes mainly attracted from high flower bud densities of the two host plant species, while the occurrence of larvae of the two lycaenid species strongly depend on micro-habitat structures like low vegetation height and density and a high proportion of bare soil, but not affect the degree of bud density (Fig. 1). These results underline that imagines and larvae of the same butterfly species prefer diverging micro-habitat conditions within the same ecosystem.

In contrast to our results that the occurrence of imagos strongly depend on flower bud density, but not the degree of egg oviposition, a study by Janz and colleagues (2005) showed an opposite trend. Here, female imagines preferably oviposited eggs at host plants with a high number of flower buds in *P. icarus*. The authors assumed that imagines become attracted by olfactory and/or visual signals (Janz et al. 2005). Similar coherences were found for *Hlicoverpa armigera* (Liu et al. 2010). Here, the authors explain this behaviour as combined nectar feeding and egg oviposition strategy, a potential advantage for the butterfly to have shorter movement distances, reduced energy consumption and subsequent lower predation pressure.

Quality of larval habitat

Our data indicate that egg oviposition rates in *P. icarus* and *P. bellargus* mainly depend on low vegetation height and a high percentage of bare soil (while flower bud density show no effect on egg oviposition). These findings are in congruence with previous work revealing that butterfly females preferably oviposit eggs on plants which are rather outstanding the surrounding vegetation (density effect), or being located at the edge of a cluster of host plants (edge effect) (Fartmann and Hermann 2006; Trautner 2006; Möllenbeck et al. 2009). This implicates that butterfly imagines are mainly laying eggs on plants which are conspicuous and accessible (Loritz and Settele 2006; Krämer et al. 2012). Here, the difference of vertical height between the selected host plant and the surrounding vegetation is assumed to be of high relevance (García-Barros and Fartmann 2009).

There exist two non-exclusive explanations how female butterflies select sites for egg oviposition: (1) Female butterflies may randomly search for host plants, but preferably select ones which are easy to find and to reach for oviposition (high-growing,

outstanding plants are easier to reach than plant individuals hidden by the surrounding vegetation); or, (2) females are actively searching for specific microstructures which may positively influence the success of larval development (selection of sites of high habitat quality—according to the ‘mother-knows-best hypothesis’, discussed in Clark et al. 2011). The first assumption becomes underlined by studies observing that butterfly females oviposit eggs even on wrong plant species being not suitable or being of low growth quality (with low levels of nutrition available) for the larvae, however, which were easy to reach (Weiss et al. 1988; Anthes et al. 2008; Goverde et al. 2008). Other studies underline the ‘mother-knows best hypothesis’, showing that female butterflies are in particular attracted by high quality plant individuals by visual and olfactory parameters (Porter 1992; Renwick and Chew 1994; Fartmann and Hermann 2006; Freese et al. 2006). For example, plant individuals with larger leaves were preferred for oviposition than plants with small leaves (Anthes et al. 2008).

Micro-habitat suitability detection with drones

During the last decades habitat suitability models (HSMs) and species distribution models (SDMs) have been successfully applied for a broad range of applications, predominantly on a continental and landscape scale (Habel et al. 2011). One reason why there is only a very limited number of studies applying HSM and SDM techniques for the characterization of micro-habitats may be a limited availability of fine scale environmental predictors, as even modern satellites produce images with a spatial resolution of several meters and varying temporal resolutions which commonly cannot be easily adjusted for specific ecological research questions on very small spatial and temporal scales (Cord and Rödder 2011; He et al. 2015). Therefore, the preference of species for specific micro-habitats was so far restricted to field observations (see introduction).

As demonstrated in this study, unmanned aerial vehicles may provide land cover information with a very high, user specified resolution, allowing a micro-habitat mapping and characterization which was not possible so far. Although the camera equipment used herein only captures three color channels, it was possible to distinguish micro-habitat types and even

subtle characteristics of preferred sites for reproduction of the butterflies (Fig. 2, Appendix S2) validated using extensive field observations. Depending on the carrying capacity of the aerial vehicle, different types of sensors can be equipped, wherein HSM predictions using multispectral aerial pictures may allow even more distinct differentiation between habitat structures including indices of moistness and surface temperature. Combined with traditional ground based ecological sampling designs as performed herein, this additional data source allows the computation and projection of HSMs into geographic space bringing autecology and spatial ecology into a new dimension.

From a technical point of view, our study shows that high resolution aerial pictures enable the detection of high-quality habitats, and thus can be used to identify areas of high relevance for species protection and areas where management action should be implemented to improve or maintain habitat quality for targeted indicator species. In consequence, unmanned aerial vehicles with high resolution cameras can be used to create valuable background data for habitat suitability models—to project knowledge from fine-scaled ecological field observations onto a large geographical range. The combination of high resolution aerial pictures with models can further be used to approve the efficiency of management strategies in the field over a larger scale. Locally assessed field data can be re-used for other areas to project habitat suitability for a specific taxon after high resolution aerial pictures were taken elsewhere.

Conservation action

Our example underlines that complete life cycles of organisms has to be taken into consideration to conduct effective conservation management, at different spatial levels (cf. Sutherland et al. 2004). Various studies showed that, particularly species demanding more than one resource as representatives of the butterfly genus *Phengaris* (see introduction), may react highly sensitive on habitat and environmental modifications (Thomas et al. 2011). According to our data, management strategies should focus on high densities of flower buds (the main nectar source for imagines), and specific micro-habitat structures for the pre-imaginal stage. The latter factor could be supported by small scale disturbances (the intermediate disturbance hypothesis, Fartmann 2006; Wallis de

Vries 2006). Furthermore, our data indicate that geographic proximity to shrubs and subsequent temporal shadow might have a positive effect on the quality of larval habitat, while a complete shadow may rather negatively affect the occurrence of larvae as the duration of larval development is strongly affected from solar radiation and temperature (Dolek and Geyer 2000; Anthes et al. 2008). This shows that, apart from small scale disturbances (which can be artificially produced via sod cutting, non-plough tillage, mowing), a habitat heterogeneity with a fine-grained mosaic consisting of open grassland intersected by shrubs may positively affect our model organisms (and many other species).

Acknowledgments We thank Sabrina Behrendt, Christine Hammel, Stefanie Künstle, Verena Smieskol and Simone Zimmermann for data collection in the field. We thank two anonymous referees for fruitful comments on a previous version of this manuscript.

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