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# Nest site preferences of the Woodlark *(Lullula arborea)* and its association with artificial nest predation

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ABSTRACT

The Woodlark is an insectivorous bird, which is listed as a priority species in Switzerland. In Valais, a stronghold of this species in the country, the birds breed in intensively managed vineyards and show a preference for parcels with ground vegetation during territory establishment. As a ground-breeder, the species is highly vulnerable to nest predation by avian and mammal predators. The aims of our study were firstly to investigate nest site preferences of the woodlark within vineyards and secondly to compare the predation risk of artificial nests dependent of ground vegetation structure. Our results point out that the Woodlark prefers patches of tall and dense ground cover within vegetated vineyard parcels and avoids parcels that have been treated with herbicides. In a follow-up experiment we conducted a study comparing the predation rate of artificial nests between bare parcels (<20% vegetated area) and vegetated parcels (>40% vegetated area). Artificial nests equipped with one quail egg were distributed pairwise between two adjacent parcels that fulfilled the upper criteria and were monitored by trail cameras during 10–12 days. Predation rate was generally low (4 predation events) and only occurred in bare parcels. These data indicate that conspicuousness of avian nests may be decreased in vegetated parcels and that the amount of vegetation can lower the predation risk on ground breeding birds - another indication for the importance of ground vegetation for a successful conservation of the endangered Woodlark in Swiss vineyards.

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## 1. Introduction

The choice of a nesting site is a crucial step in the habitat selection process for territory establishment in birds (Martin, 1993). Breeding birds have to assess a multitude of biotic and abiotic factors, such as habitat composition (Martin, 1993; Parker, 1986), parasite pressure (Loye and Carroll, 1998) and microclimatic conditions (Ardia et al., 2006; Dawson et al., 2005), which may impact reproductive success. The risk of nest predation, in particular, can endanger the whole brood and even the incubating parents and its importance as one of the primary causes of nest loss has increasingly been the focus of research in the past years (e.g. Martin, 1993; Nice, 1957; Ricklefs, 1969; Seibold et al., 2013). The risk of nest predation not only depends on habitat features (Martin, 1993) but also on the abundance and the level of dietary and habitat specialization of nest predators (Renfrew and Ribic, 2003; Weidinger, 2009). Birds have been shown to modify their selection of breeding habitat and nesting site with respect to the prevailing predation pressure (Eggers et al., 2006; Latif et al., 2012; Lima, 2009; Moller, 1989), thereby trying to reduce the risk of nest loss. Structural heterogeneity and vegetation density around the nest, both may contribute to a reduction of the predation risk by lowering nest visual detectability and accessibility (Gillis et al., 2012; Gomez-Serrano and Lopez-Lopez, 2014; Harrison et al., 2011; Martin, 1993). However, nest concealment may also come with a concealment of potential predators. This may represent an additional risk, especially for nestlings and parents if they are not able to detect and adapt their behaviour in face of an approaching predator. Birds selecting a nesting site must therefore incorporate multiple cues and factors in their decision-making process in order to maximise the reproductive success (Götmark et al., 1995; Martin, 1993).

The Woodlark *Lullula arborea* is a multi-brooded, ground nesting

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passerine (Brambilla and Rubolini, 2009), occurring throughout the Palearctic realm. It is included in to the red-list of Switzerland (cat. B2, Keller et al., 2010) while not endangered globally (Burfield and van Bommel, 2004) and even having populations increasing for instance in Britain (Conway et al., 2009), Italy (Campedelli et al., 2012), France and the Netherlands (Burfield and van Bommel, 2004). Woodlarks mainly occupy semi-natural heathlands (Mallord et al., 2007; Praus et al., 2014), field-forest ecotones (Schaefer and Vogel, 2000), pine plantations (Bowden, 1990), as well as olive groves (Castro-Caro et al., 2014) and vineyards. When foraging, Woodlarks prefer microhabitats with some amounts of bare ground, as sparse vegetation increases the prey availability for the birds (e.g. Arlettaz et al., 2012; Bowden, 1990; Mallord et al., 2008) what has been shown to be beneficial also for many other ground-foraging insectivorous bird species (Menz et al., 2009; Schaub et al., 2010). In contrast, Woodlarks have been shown to prefer clumps of denser and taller vegetation in heathlands (Harrison and Forster, 1959; Mallord et al., 2007) and at forest edges for building their ground nest (Schaefer and Vogel, 2000). These contrasting ecological requirements for territory settlement are met where habitat and vegetation exhibits a certain degree of heterogeneity (Campedelli et al., 2015; Sirami et al., 2011). Its current population size in Switzerland is estimated at 250–300 breeding pairs of which around the half occurs in semi-natural grasslands (pastures, steppes) whereas the other half mainly breeds in vineyards on the south-facing slopes along the Rhône valley (Arlettaz et al., 2012). Woodlarks use vineyards in this region as a combination of secondary and surrogate habitat and do not occur in vineyard landscapes in most other parts of Switzerland. There, about 90% of vineyards have a bare appearance, i.e. they have little or no ground cover: ground vegetation is systematically treated with herbicides or partly also mechanically removed. Yet, due to criticism of herbicide use based on study results showing e.g. weed resistance to glyphosate (Evans et al., 2016; Goh et al., 2016), or the controversial about the carcinogenic effects of this herbicide (George et al., 2010), the pressure to reduce herbicide or pesticide applications in general is increasing constantly. Thus, more and more winegrowers are looking for new management techniques and are adapting a more nature-friendly, extensive management of their vineyards. It is not known how these contrasting management practices in vineyards affect the nesting preferences and reproductive success of Woodlarks.

Here we investigated nest site preference patterns of Woodlarks inhabiting vineyards with respect to the surrounding vegetation cover, as well as the risk of nest predation dependent on the vegetation structure. This information is crucial to propose vineyard management practices that can fulfil the different habitat needs and especially the breeding requirements of this endangered bird species in Switzerland.

## 2. Methods

### *2.1. Study area*

The study was carried out in five municipalities in the upper Rhône valley in Valais, Switzerland (Miège 46°19′N 7°33′E, Salgesch 46°18′N 7°34′E, Venthône 46°18′N 7°32′E, Randogne 46°19′N 7°30′E and Chamoson 46°20′N 7°22′E). In all these sites vineyards represent the predominant agricultural land use type. They are mostly managed intensively, having no or limited ground vegetation cover, which results in mosaics of many bare vineyards, punctuated with few vegetated vineyard parcels that harbor ground vegetation cover. They are mainly located on sun exposed slopes north of the Rhone river whereas in the steeper zones they are interspersed with patches of dry forest and rocky steppe (Arlettaz et al., 2012). Approximately half of the Swiss Woodlark population occurs in Valais, most of them breeding in vineyards from March until July (Arlettaz et al., 2012; Sierro and Arlettaz, 2003). The nest-site preference study was carried out during the breeding season (March–May) in 2013, 2015 and 2016, whereas the predation study was conducted during April 2014. Both studies were realized in different years but since conditions in regard to vegetation structure (cover and height) and climate do not vary strongly between years we believe that inter-annual differences in nest-site preferences and predation rate are not relevant for the conclusions of the study.

### *2.2. Mapping of nest site characteristics*

Woodlarks were mist-netted, ringed and equipped with radio transmitters (Holohil DB-2, 0.95 g, 60p/min, Canada; transmitter is ~3.5% of body weight) using leg-harnesses in the years 2013, 2015 and 2016 (46 birds in total: 13 in 2013; 19 in 2015; 14 in 2016). We did not report any behavioural changes or negative effects on the welfare of the tagged birds due to the transmitters during the wole radio-tracking period (30 days each bird), whereby three individuals lost their transmitter after some days due to malattachment of the harness. The birds have been radio-tracked for approximately 1 month during their main breeding period (March–May), as limited by the lifespan of the battery. In total 21 nests were found for 19 individuals (7 in 2013, 10 in 2015 and 4 in 2016), whereas for two birds two nests were found during the same breeding season (replacement clutches or second broods). As all nests were detected during radio-tracking, any detection probability bias due to different vegetation structures, i.e. lower detection probability of nests in denser vegetation, can be excluded. For the nest site preference analysis we mapped the ground vegetation cover and the vegetation height on two different spatial scales. Firstly, on a so called ‘parcel scale’, where we compared the nest parcel to all adjacent neighbouring vineyard parcels which thereby served as controls, whereas parcel size varies considerably within our study area (range: 51–17 109 $m^2$; mean = 1256 $m^2$; QGIS data, QGIS Development Team, 2015). Secondly, on a ‘nest scale’ where we compared the same vegetation features in a 1 $m^2$ square around a nest to four randomly chosen 1 $m^2$ squares within the same nest parcel in order to assess the small-scaled features preferred for nest placement within a vineyard parcel. We used the parcels as spatial units given that vineyards can clearly be separated from each other spatially due to contrasting management practices (e.g. ground vegetation structure, vine plant attachment techniques, arrangement of the vine rows). Vegetation cover was recorded by visually estimating the percentage of area covered by plants (ranging from 0 to 100%, in steps of 5%) for both spatial scales. To estimate the mean vegetation height we used the ‘direct measurement method’ (Stewart et al., 2001) by taking the mean from four different points measured per parcel and two per 1 $m^2$ plot, respectively.

### *2.3. Recording of predation events*

To investigate the effects of ground vegetation on nest predation, we performed experiments using artificial nests made out of on-site pieces of grass, equipped with one quail egg. These types of studies are used to give a general relative estimate of the nest predation risk of ground nesting birds in relation to environmental conditions, in our case ground vegetation, but cannot or only approximately account for factors such as species, parental behaviour, species-specific nest odour or clutch size.

We used a design where we always compared nest predation rate of artificial nests placed in two adjacent parcels that differed in the type of ground management. Such a unit is called a treatment pair where one parcel of the treatment pair was being predominantly bare (ground vegetation removal, either chemically or mechanically) and the other having ground vegetation (hereafter called vegetated parcel). The bare and vegetated parcels had to fulfil the following criteria: *i)* bare parcels had to contain less than 20% ground vegetation cover, whereas vegetated parcels had to contain a minimum of 40% ground vegetation cover; *ii)* parcels within a treatment pair were of similar size (less than 20% size difference); and *iii)* the two nest locations within each treatment pair had to be at least 20 m apart from each other. Additionally, there had to be a minimum distance of 150 m between the different treatment pairs. In total we had 27 treatment pairs (27 artificial nests in vegetated parcels and 27 artificial nests in bare parcels), resulting in a total of 54 artificial nests. To record predation events we used pole-mounted trail cameras (Reconyx PC900) that were placed at a distance of 1–2 m from the artificial nests. After installing the camera, we left the site in the opposite direction, thereby avoiding dead-end tracks (Praus and Weidinger, 2010). The cameras were programmed to take three consecutive pictures whenever any movement of an animal triggered the camera and additionally one picture every 15 min was recorded. Each trial of a treatment pair lasted for 10–12 days, which approximates the incubation period of Woodlarks (Praus et al., 2014). After a predation event had occurred, the predated nest and the intact nest of the same treatment pair were removed, in order to exclude any learning effects of predators. Thus, each site was only used once during the breeding season.

Additionally, we estimated the abundance of predators in relation to the vineyard ground vegetation cover and identified the predatory species. For this purpose we counted the number of potential predators recorded by our trail cameras using the following criteria: Firstly, predators were only counted when passing within the first row visible, i.e. until the next row of vine plants. This is because ground vegetation and vine plants conceal predators in successive vineyard rows and thereby reduce the probability of triggering the trail cameras. Secondly, to avoid counting the same predator within a short time period, we discarded the photos that were taken within 30 min after the successful photographic capture of a given predator. Also, only predators that passed by the artificial nest without showing any signs of detecting it, were counted for this analysis. Potential Woodlark predators in our study area are the Red Fox (*Vulpes vulpes*), the European Badger (*Meles meles*) and several species of corvids: Eurasian Magpie (*Pica pica*), Eurasian Jay (*Garrulus glandarius*), and the Carrion Crow (*Corvus corone*) (also according to Praus et al., 2014).

### 2.4. Statistical analyses

All analyses were performed using the open source software R, version 3.0.2 (R Development Core Team, 2013). Nest-site characteristics at the parcel and nest scales were analysed using generalized linear mixed models (glmer - R package “lme4”; Bates et al., 2015) with a binomial error distribution, nest as random factor and vegetation cover % and vegetation height as explanatory variables. Both variables were standardized and transformed, if necessary. Collinearity between both habitat variables was tested using the Spearman's correlation coefficient. Variation in predation rate of artificial nests was analysed using the Kaplan-Meier method (R package “survival”; Therneau, 2014). This non-parametric survival time analysis allows calculating and comparing the survival rate of two treatment groups given a sample size large enough (Kaplan and Meier, 1958; Mauser et al., 1994) and has been applied in several ornithological studies (Aldridge and Brigham, 2001; Anders et al., 1997; Mauser et al., 1994). This statistical approach is appropriate compared to the widely used Mayfield method (Nur et al., 2004), which is intended to overcome the bias associated with finding nests at different stages - a factor not relevant in our experimental study design - as all our nests were artificial and thus started at the same stage. Though, as sample size for this analysis is rather low, the results are only indicative and not generalizable. Survival times were measured from the time of nest-setup either to the predation event or until the end of the experiment. Survival probability is then calculated for each time interval (days) as the number of nests surviving divided by the number of nests at risk (i.e. the total number of nests minus the number of nests predated). The comparison of the survival curves in both parcel types (bare vs. vegetated) is based on the log-rank test. When analysing the abundance of predators in respect to parcel type (bare vs. vegetated) we used generalized linear mixed models (R package “nlme”; Pinheiro et al., 2012) with a Poisson error distribution, the type of parcel as explanatory variable and the identity of the treatment pair as random factor.

## 3. Results

### 3.1. Nest site preference

Nineteen out of 21 nests found were located in vegetated parcels (mean ground vegetation cover ± standard error: 67.11 ± 13.1%, range: 30–80%) with a relatively tall vegetation (mean height: 23.58 ± 13.5 cm, range: 6–50 cm, $N = 21$ parcels) while the control parcels had a mean ground coverage of 40.12 ± 30.9% (range: 0–100%) with a mean vegetation height of 11.61 ± 13.4 cm (range: 0–70 cm, $N = 97$ parcels). The multivariate mixed effect models confirmed: the surrounding parcels had significantly lower ground vegetation cover (estimate ± SE = −0.83 ± 0.38, $z = -2.18$, $P = 0.029$; Fig. 1a) and lower vegetation height (−1.14 ± 0.51, $z = -2.23$, $P = 0.025$; Fig. 1c) than the Woodlarks' nest parcels, whereas these two variables were inter-correlated (Spearman's correlation coefficient of vegetation cover % and vegetation height = 0.63). The same pattern based on multivariate mixed effect models was found at the nest scale, where nest sites had more ground cover (estimate ± SE = 0.94 ± 0.4, $z = 2.38$, $P = 0.017$; Fig. 1b) and a considerably taller vegetation (1.28 ± 0.43, $z = 2.99$, $P < 0.01$; Fig. 1d) than control sites within the same parcel. Nest sites showed a mean ground cover of 59.52 ± 16.27% (range: 25–90%) and an average vegetation height of 18.48 ± 12.62 cm (range: 7–50 cm, $N = 19$ nest sites), whereas the control sites showed, on average, 27.95 ± 27.94% (range: 0–100%) of ground vegetation cover with a mean vegetation height of 8.01 ± 8.6 cm (range: 0–50 cm, $N = 76$ control sites).

### 3.2. Nest predation

In total, we recorded four predation events from 54 artificial nests: one nest was predated by Red Fox (*Vulpes vulpes*), two by Eurasian Magpies (*Pica pica*) and one by Eurasian Jay (*Garrulus glandarius*). We obtained an overall survival rate of 0.9 ± 0.04 (95% CI: 0.86–0.99) for the 12-day period. All mentioned predation events took place in bare vineyards, which could indicate a significantly higher predation rate compared to green vineyards ($\chi^2 = 4.2$ on 1 df, $P = 0.04$; Fig. 2). Overall survival rate over the 12 days was 1 in the vegetated vineyards while it was 0.85 ± 0.07 (95% CI: 0.73–0.99) in the bare vineyards. Overall, we encountered 52 potential predators in the 54 vineyard parcels with a mean (±SD) abundance of 0.87 (±1.76) in vegetated and 1.39 (±3.38) in bare vineyards. There was no significant effect of vineyard management type on predator abundance (estimate ± SE = −0.47 ± 0.29, $z = -1.65$, $P = 0.10$).

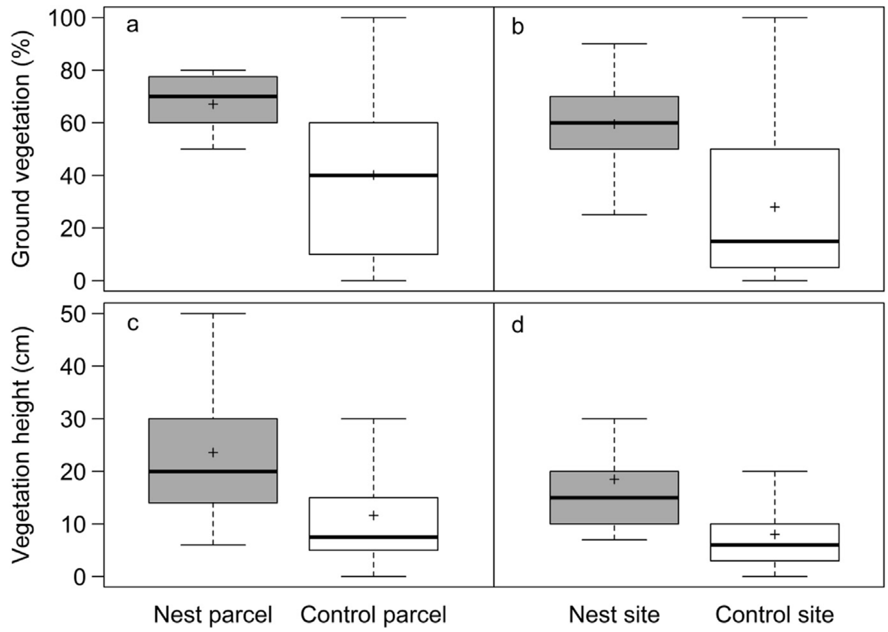


**Fig. 1.** Ground vegetation cover (upper panel) and vegetation height (lower panel) in vineyard parcels (Valais, Switzerland) with Woodlark nest ($N = 21$) and adjacent parcels (a, c; parcel scale); and at nest and randomly chosen control sites within the nest parcel (b, d; nest-site scale). The horizontal lines show medians, cross the means, boxes the standard errors, and error bars the 95% confidence limits. Shown are raw data while the model estimates are given in the results section.

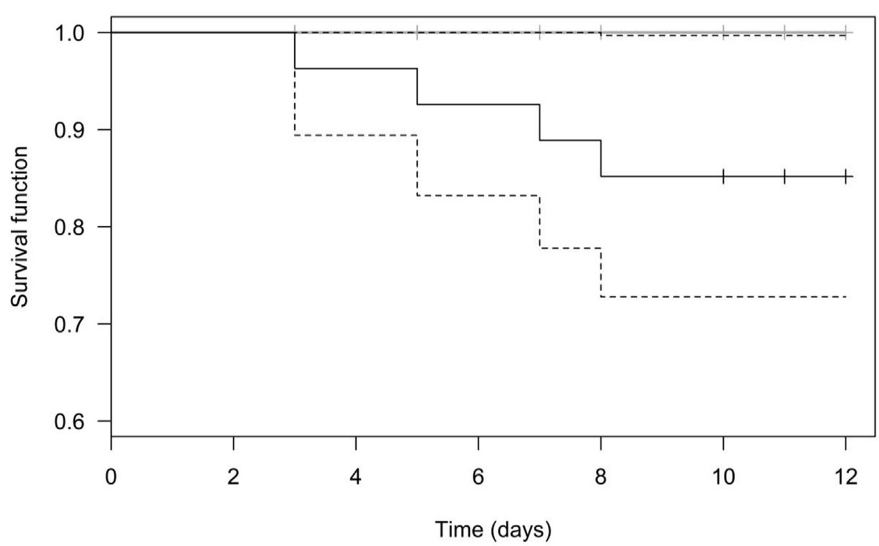


**Fig. 2.** Kaplan-Meyer survival estimates of artificial nests where the grey line depicts the flat trajectory in green parcels and the black line (with 95% confidence intervals as dotted lines) the declining trajectory within mineral parcels. While the steps illustrate the predation events, the short vertical lines indicate whenever a treatment pair was terminated.

## 4. Discussion

Our study renders preliminary data highlighting the importance of ground vegetation in vineyards for the successful reproduction of Woodlarks. Firstly, our results show that for nesting Woodlarks have a preference for vegetated vineyard parcels with considerably dense and tall ground vegetation around the nest site. Second, artificial nests in bare vineyards with no or restricted ground vegetation cover indicated a higher predation rate compared to artificial nests in vegetated vineyard parcels. But given the small sample sizes of the nest predation study, we consider our results to be preliminary and indicative. Our results about the nest sites preference in ground vegetated vineyards complement earlier findings from studies conducted in habitat types different from vineyards (Bowden, 1990; Castro-Caro et al., 2014; Harrison and Forster, 1959; Mallord et al., 2007). Although Woodlarks select patches of bare ground when foraging due to enhanced prey accessibility, as also established for other terrestrially foraging insectivorous birds (Arlettaz et al., 2012; Bowden, 1990; Mallord et al., 2007; Schaub et al., 2010; Tagmann-Ioset et al., 2012; Vickery and Arlettaz, 2012), they require a denser and especially taller vegetation cover for nesting (Harrison and Forster, 1959; Mallord et al., 2007). In light of the results we obtained about artificial nest survival dependent on vegetation cover, this seems to be dictated by nest concealment against predators; yet, enhanced microclimatic conditions cannot be ruled out (Bowden, 1990;

Harrison and Forster, 1959; Mallord et al., 2007; Sirami et al., 2011).

Interestingly, predation rate at the egg stage was generally low in our artificial nest experiment, which matches observations from real Woodlark nests where they found a considerable higher predation rate at the chick stage compared to the egg stage (Eyre and Baldwin, 2014; Praus et al., 2014). Our results indicate that nests in vegetated parcels have a very low risk of being depredated, what leads to two, non-mutually exclusive hypotheses that could explain the increased risk of predation in relation to a reduced ground cover: a higher abundance of predators in bare parcels; a higher visual conspicuousness of nests; or an interaction of these two factors. As there was no evidence that predators were more abundant in vineyards with little or no ground vegetation compared to vegetated vineyards we conclude that increased visual conspicuousness of nests may account for an increased predation rate. In our study, three out of the four predation events were caused by birds, further indicating that the vegetation cover might be a form of defence to protect the nests from predators who hunt on sight (Martin, 1993; Svobodovà et al., 2004).

Nonetheless, the risk of predation might be an interaction between predator density and detection probability of the nest, where both factors, and their interaction, fluctuate seasonally in relation to environmental conditions, vineyard management and the stage of the breeding cycle. In particular, herbicide application or ground vegetation mowing might suddenly and dramatically alter the surrounding habitat. We surmise, based on field observations, that such farming practices can lead to situations where nests end up being surrounded with little or no vegetation and thus might then be particularly prone to predation. Further, these treatments lead to a reduction of total suitable habitat available for the nesting of this species, what may have consequences on the overall reproductive success on a population level.

Moreover, predation type is likely to vary during the breeding cycle. While visually orienting predators, such as corvids, may be at an advantage when ground cover is low (Eyre and Baldwin, 2014; Praus et al., 2014), olfactory or acoustic hunting predators such as carnivores may have a stronger impact during the nestling stage (Eyre and Baldwin, 2014). As the observed predation rate on artificial nests was low and we only carried out experiments during the egg stage, we cannot infer any general predation patterns on the Woodlark (Wilson et al., 1998). These preliminary findings indicate that in Switzerland ground-breeding birds such as the Woodlark may benefit from green vineyard parcels, partly due to a reduced risk of nest predation. This points out that certain amounts of ground vegetation cover not only provide suitable foraging conditions to terrestrially feeding Woodlarks (Arlettaz et al., 2012; Bowden, 1990), but also represents a crucial resource for nesting, whereas the vegetation density and structure differ between foraging and nesting sites. These contrasted habitat requirements by Woodlarks may readily be fulfilled in certain heterogeneous natural or semi-natural landscapes, but probably pose a challenge among vineyard monocultures, as here the habitat composition is entirely dependent on the viticulturist's management. The key habitat and vegetation heterogeneity required by the differential habitat needs of Woodlarks could be met where modern vineyard management allows partial vegetation cover to grow on the ground surface, what indicates the need for an extensification of intensive agricultural areas, especially vineyards, for a careful conservation of biodiversity (Carrete et al., 2002; Jedlicka et al., 2011). This mixture of sparse and dense ground vegetation could be achieved by several different and partly complementary management practices: (a) by avoiding commercial seed mixtures, which tend to result in a dense species-poor cover, but instead by allowing spontaneous, diverse vegetation that will vary in structure and density within the parcel; (b) herbicide application could be limited to the area below the vine plants, resulting in a small scaled, heterogeneous vegetation structure (as the area between the vine rows would be vegetated, interspersed by bare rows); (c) mowing, ploughing or herbicide application could be limited to every second row in order to generate a vegetation mosaic within a parcel. Finally, also on a landscape scale, a certain heterogeneity seems to be beneficial to meet the Woodlarks habitat needs (Campedelli et al., 2015; Sirami et al., 2011) what implies that vegetation structure should not only vary within but also among vineyard parcels.

## Author contributions

Buehler R., Bosco L., Jacot A.: design of the study, acquisition, analysis and interpretation of data, drafting and revising the manuscript.

Arlettaz R.: contributions to the manuscript by revising and commenting on draft versions.

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