Soil management of olive groves has contrasting effects on nest densities and reproductive success of tree-nesting passerines

Juan Carlos Castro-Caro 1, Isabel C. Barrio 2 and Francisco Sánchez Tortosa 1

1University of Córdoba, 2Agricultural University of Iceland

ABSTRACT. Agri-environmental measures aim at mitigating the negative impacts of modern agriculture on farmland biodiversity. For example, soil management practices can positively influence the abundance and diversity of songbirds in olive groves by enhancing habitat and food availability. However, little is known about their potential implications on the breeding success of these species. We monitored nest density and breeding performance of tree-nesting birds in 17 olive groves of southern Spain under two contrasting soil management regimes (with and without herbaceous cover) over three years. We analyzed breeding success by examining the transitions between different stages of the breeding cycle for three common cardueline finches: Common Linnet (Linaria cannabina), European Greenfinch (Chloris chloris), and European Serin (Serinus serinus).

Breeding success of songbirds was low (19% of 88 nests for L. cannabina, 16% of 196 nests for C. chloris, and 38% of 234 nests for S. serinus). Many nests were abandoned prior to egg laying and nesting failure was highest between egg laying and hatching. Nest predation (56.6%) was the main cause of nest loss. Although soil management regimes did not influence breeding success, the presence of herbaceous cover had opposing effects on nest densities of the three species: groves with herbaceous cover had higher nest densities for greenfinches, lower for serins, and this treatment had no effect on Common Linnet. Other factors, like disturbances due to management activities or interannual weather variation may have a larger impact on nesting success than soil management regimes, at least for some species and for specific stages of their breeding cycle. The fact that nest densities of some birds were negatively affected by soil treatments associated with agri-environmental actions aimed at benefiting biodiversity raises the question of the general applicability of these measures for conservation.

Key Words: biodiversity; cardueline finches; herbaceous cover; nest disturbance; nest predation; Mediterranean agroecosystem; Passeriformes

La gestion des sols d'oliveraies a des effets différents sur la densité de nids et le succès de reproduction de passereaux nichant dans les arbres

RÉSUMÉ. Les mesures agro-environnementales visent à atténuer les effets négatifs de l'agriculture moderne sur la biodiversité des terres agricoles. Par exemple, les pratiques de gestion des sols peuvent influer positivement sur le nombre et la diversité des oiseaux chanteurs dans les oliveraies en améliorant l'habitat et la disponibilité de nourriture. Cependant, on en sait peu sur leurs conséquences potentielles sur le succès de reproduction de ces espèces. Nous avons suivi la densité de nids et le succès de reproduction d'oiseaux nichant dans les arbres dans 17 oliveraies du sud de l'Espagne sous deux régimes opposés de gestion des sols (avec ou sans couvert herbacé) pendant trois ans. Nous avons analysé le succès de reproduction en examinant les transitions entre les différents stades du cycle de reproduction pour trois carduelinés communs: la Linotte mélodieuse (Linaria cannabina), le Verdier d'Europe (Chloris chloris), et le Serin cini (Serinus serinus). Le succès de reproduction de ces oiseaux était faible (19% des 88 nids pour L. cannabina, 16% des 196 nids pour C. chloris, et 38% des 234 nids pour S. serinus). De nombreux nids ont été abandonnés avant la ponte et l'échec de nidification était le plus élevé entre la ponte et l'éclosion. La prédation des nids (56,6%) était la cause principale de perte de nids. Bien que les régimes de gestion des sols n'aient pas influé sur le succès de reproduction, la présence d'un couvert herbacé a eu des effets opposés sur la densité de nids des trois espèces: les bosquets avec couvert herbacé avaient une densité de nids plus élevée pour les verdiers, plus faible pour les serins, et ce couvert n'a eu aucun effet sur les linottes. D'autres facteurs, comme les perturbations dues aux activités de gestion ou les variations météorologiques interannuelles, peuvent avoir un impact plus important sur le succès de nidification que les régimes de gestion des sols, du moins pour certaines espèces et à des étapes spécifiques de leur cycle de reproduction. Le fait que la densité de nids de certains oiseaux ait été négativement affectée par le traitement des sols dicté par des actions agro-environnementales visant à favoriser la biodiversité soulève la question de l'applicabilité générale de ces mesures pour la conservation.

Key Words: biodiversité; cardueline finches; herbaceous cover; nest disturbance; nest predation; Méditerranée agroécosysteme; Passeriformes

Correspondent author: Juan Carlos Castro-Caro, Spain, cascajuca@gmail.com
INTRODUCTION

The detrimental impact exerted by intensive agriculture on ecosystems and the environment is widely recognized and is predicted to further increase through the 21st Century (Egli et al. 2018). In Europe, agricultural intensification has resulted in severe declines of farmland bird populations (Emmerson et al. 2016), with particularly concerning effects on many common and widespread farmland species (Inger et al. 2015).

Permanent crops are the third largest farming system by area in Europe (EUROSTAT 2019) and have experienced strong intensification over the last decades (Emmerson et al. 2016). Intensification in permanent crops, like olive groves, is usually associated with increased fertilizer and pesticide inputs, deep ploughing, homogenization of biotic communities, and loss of environmental heterogeneity (Rey 2011, Sokos et al. 2013). This situation is exacerbated by the exemption of these crops from the “greening” measures introduced with the 2013 reform of the Common Agricultural Policy, specifically designed at a European level to reduce the negative impact of agriculture on the environment (Pe‘er et al. 2014).

In the Mediterranean Basin, olive groves are one of the primary agro-ecosystems and they are important winter quarters and breeding ranges for numerous European bird species (Rey 2011). In Spain, the largest area of olive farming in Europe, 2.5 million ha are dedicated to this crop. In recent decades, agricultural intensification and changes in land use have replaced the traditional mosaic structure of olive groves with monocultures that result in homogeneous landscapes (Kizos and Koulouri 2006, Sokos et al. 2013). This so-called conventional farming, involving the intensive use of agrochemicals, has become the most common production system (85% of the crop area), which has led to significant negative environmental consequences including water pollution, soil erosion, and loss of farmland biodiversity (Morgado et al. 2020).

In this highly intensive scenario, the only agri-environmental measure now in practice is the promotion of herbaceous cover within the groves. Herbaceous cover promotes farmland bird diversity (Muñoz-Cobo et al. 2001, Muñoz-Cobo 2009, Castro-Caro et al. 2014a, Castro-Caro et al. 2015, Rey et al. 2019), through increasing structural complexity and providing resources for foraging birds (Wilson et al. 1999, Vickery et al. 2009). For example, herbaceous cover in olive groves delivers increased biomass of arthropods (Carpio et al. 2019), and food resources are an important determinant of selection of breeding territories (Muñoz-Cobo 2009). In addition, the presence of herbaceous cover can increase the reproductive success of breeding birds in other systems, like the forest-tundra ecotone (Norment 1993) or sagebrush communities (DeLong et al. 1995), but little is known about their effects in intensively managed crops. In olive groves, studies using artificial nests showed that herbaceous cover can reduce the rate of nest predation (Castro-Caro et al. 2014b), which is one of the major reasons for reproductive failure of birds (Evans 2004). However, there is no information on the effects of these agri-environmental measures on different stages of the breeding cycle based on monitoring of real nests.

In this study we assessed the effects of soil management regimes, i.e., use of herbaceous cover, on breeding success of tree-nesting songbird communities of conventional olive groves in southern Spain. We measured nest densities and reproductive success of passerine birds in olive groves with and without herbaceous cover. We analyzed breeding success separately for each stage of the breeding cycle: egg laying, hatching, and fledging, because these stages can be differently sensitive to predation (e.g., Halupka 1998). If herbaceous cover provides a better habitat for breeding birds, by either increasing food availability or reducing predation risk, we would expect (1) higher nest densities and (2) higher breeding success in olive groves with herbaceous cover. We also expected that (3) the effects of herbaceous cover could vary for different phases of the breeding cycle, if herbaceous cover provides resources that are critical for a particular phase, e.g., nestlings’ diet (Gil-Delgado et al. 2009) or alters predation rates on specific phases, e.g., reduced egg predation (Castro-Caro et al. 2014b).

METHODS

Study area and study species

The study was conducted over three years (2010–2012) in the Guadalquivir Valley, SE Córdoba province, southern Spain (37° 59′ N, 4°17′ W). The climate is typically Mediterranean, with warm dry summers and cool humid winters. Mean annual temperatures range between 15 °C and 18.5 °C, and annual average precipitation is 550 mm (Aparicio 2008). Olive farming in this area is intensive, with heavy usage of chemicals (herbicides, fungicides, and insecticides), high levels of mechanization, and water supplementation. The resulting landscape is dominated by large patches of monoculture and is considered a “simple” landscape (sensu Batáry et al. 2011) because the semi-natural habitat patches that remain account for < 10% of the area.

To determine the impact of herbaceous cover on tree-nesting songbird communities, we assessed the reproductive success of passerine birds in seventeen olive groves, eight with and nine without herbaceous cover. Olive groves were selected based on the permission to access the land given by the land owners. All olive groves were in flat areas, had trees > 100 years old at a density of 85%, but was consistent within groves over the 3-yr study period. Olive groves were in flat areas, had trees > 100 years old at a density of 85%, but was consistent within groves over the 3-yr study period. In the second half of May, the herbaceous cover was mowed and plant-free by the localized application of herbicides. The amount of area covered by herbaceous cover varied among groves (20–85%) but was consistent within groves over the 3-yr study period. In the second half of May, the herbaceous cover was mowed and left on site. Not all groves were sampled every year, but survey effort (number of olive trees sampled) did not vary significantly across years (ANOVA, F2,9 = 1.337, p = 0.310) and groves with and without herbaceous cover (ANOVA, F1,10 = 0.012, p = 0.916).

Nest searching and monitoring

Our study focused on tree breeding songbird (passerine) communities (Table 1). Our analyses focused on three Cardueline finches that are the most common tree-nesting breeding birds in our study area: European Serin Serinus serinus, European Greenfinch Chloris chloris and Common Linnet Linaria cannabina.

Intensive nest searching and monitoring was conducted during the breeding period by the same observer (JCCC), between 20
Mar 25 Jun 25 2010–2012. Nest densities (nests/ha) were calculated for each olive grove, as the number of nests divided by the area, estimated based on the number of trees surveyed. Trees were visually inspected for nests by carefully walking around each tree to find nests located in the outer part and by walking under the crown, next to the trunk to find nests located in the inner part of the trees. Once located, nests were georeferenced using a handheld GPS (Garmin e-Trex) and active nests were monitored every four days when possible. To minimize disturbance to nests and reduce the time spent on each nest, we used a small mirror attached to a long pole. Nest monitoring data included nest stage (nest constructed, presence of eggs, presence of nestlings, and evidence of fledglings, i.e., feces on the edges of the nest; Fig. A2.1), and bird species, if known. Only the final fate was recorded for each nest and therefore, no data is available for when changes between nest stages occurred. Whenever possible, evidence of nest predation was recorded, e.g., eggshell remains or nest disturbance (Fig. A2.1); nest failure to predation could not always be attributed with certainty and in such cases cause of nest failure was recorded as unknown, so our measure of predation represents a conservative estimate of nest predation rates.

Table 1. Number of nests of different species of songbirds in olive groves of southern Spain with and without herbaceous ground cover. From the total number of nests, those that were successful are indicated in brackets. Daggers indicate the most abundant species for which separate analyses were conducted.

| Species                  | Total | without herbaceous cover | with herbaceous cover |
|--------------------------|-------|--------------------------|-----------------------|
| Linaria cannabina†       | 57(19)| 28(4)                    | 29(15)                |
| Carduelis carduelis      | 7(4)  | 3(1)                     | 4(3)                  |
| Chloris chloris†         | 77(5) | 14(1)                    | 63(4)                 |
| Cyanoptica cooki         | 15(2) | 3(0)                     | 12(2)                 |
| Fringilla coelebs        | 2(2)  | 3(1)                     | 5(3)                  |
| Lanius senator           | 1(1)  | 45(12)                   | 46(13)                |
| Serinus serinus†         | 172(62)| 62(27)                   | 234(89)               |
| Sylvia melanocephala     | 4(1)  | 0(0)                     | 4(1)                  |
| Turdus merula            | 0(0)  | 1(0)                     | 1(0)                  |
| unknown                  | 47(1) | 71(2)                    | 118(3)                |
| Total                    | 363(95)| 357(70)                  | 720(165)              |

Probabilities of transition between different nest stages were defined as the proportion of nests in a particular stage given the number of nests in the previous stage: the probability of egg laying was defined as that of a (constructed) nest of having eggs, the probability of hatching as that of a nest with eggs of having nestlings, and the probability of fledging as that of nests with nestlings of showing presence of fledging. Overall breeding success was defined as the probability of a (constructed) nest having one or more young fledged from it. It is important to note that these values represent naïve estimators of nest success (sensu Stanley 2000) because unfortunately we did not have information on the time for which each nest was monitored, i.e., exposure days, that would allow us calculate daily nest success rates. Although these estimates of apparent nest success are known to be positively biased because successful nests have a higher probability of being detected than failed nests (Jehle et al. 2004) they still provide an estimate of breeding success.

**Statistical analyses**

Descriptive values are presented for all nests (including those for which bird species was unknown) and separately for the three cardueline species. Statistical analyses were conducted for each of these species separately, because different species can be subjected to different selection pressures, like predation or competition, at different phases of the breeding cycle. Similar analyses for other species were not possible because too few nests were found (less than 10 nests per grove type). Differences in nest density between olive groves with and without herbaceous cover were assessed using linear models (LM), where nest density for each species in each olive grove was the response variable, and cover and year were included as fixed effect factors. Differences in transition probabilities were modeled using generalized linear mixed effects models (GLMM), where transitions (egg laying, hatching, fledging, or overall nest success) were included as Bernoulli distributed response variables, cover and year were included as fixed effect factors, and olive grove was included as a random factor. In cases where year had a significant effect on the response variable, the significance of the factor was assessed by comparing the model with and without year, and Chi-squared values are reported. All analyses were conducted in R 4.0.1 (R Development Core Team 2020). Means and standard errors are reported in the text.

**RESULTS**

A total of 15,339 olive trees were surveyed over three breeding seasons; 720 nests were recorded from at least 9 bird species (Table 1). Nest densities of *S. serinus* were significantly lower in groves with herbaceous cover, significantly higher in the case of *C. chloris*, and did not differ between olive groves with and without cover in the case of *L. cannabina* (Table 2). Year of sampling did not affect nest densities in any of the models (in all cases p > 0.289; Table A3.1).

Table 2. Nest densities for the most common breeding songbirds in olive groves with and without herbaceous cover of southern Spain: *Linaria cannabina*, *Chloris chloris*, and *Serinus serinus*. Comparisons between olive groves with and without herbaceous cover were assessed using linear models (t values and p-values are shown).

| Species                  | with cover | without cover | t     | p     |
|--------------------------|------------|---------------|-------|-------|
| Linaria cannabina        | 1.37±0.69  | 2.50±1.03     | 1.68  | 0.104 |
| Chloris chloris          | 6.32±2.42  | 2.67±1.04     | -2.935| 0.007 |
| Serinus serinus          | 3.34±1.19  | 8.81±3.21     | -3.105| 0.004 |

Overall breeding success ranged between 19.3% for *L. cannabina* and 38.0% for *S. serinus*. Year did not influence breeding success for any of the focal species separately (Table A3.2). Nest failures (555 nests) could be unequivocally attributed to predation in 56.6% of the cases (314 nests). The probability of egg-laying once a nest was constructed ranged between 47 and 57% (Fig. 1). For *C. chloris* there was a trend toward increased probabilities of egg laying in groves with herbaceous cover (GLMM, p = 0.093; Fig. 1). In the case of *S. serinus*, year influenced the probability of egg laying (GLMM, Chi-squared = 6.62, p = 0.037; Table A3.2), with 2012 having lower probability compared to 2010 (Fig. 1). The presence of herbaceous cover did not influence the probability of...
Fig. 1. Nest stages and transitions identified in this study (egg laying, hatching, and fledging, and overall breeding success) for all bird species, and for the most common breeding songbirds in olive groves of southern Spain: *Linaria cannabina*, *Chloris chloris*, and *Serinus serinus*. Observed transition probabilities and overall breeding success (percentages and number of successful nests out of the total in brackets), and the effect of herbaceous covers (estimates±SE and p-values) on each stage are indicated. When year had a significant effect, the model estimate±SE and p-value for 2012 (relative to 2010) are indicated in square brackets. Significant effects are indicated in bold. “--” indicates that the model could not be calculated because of insufficient sampling size.

hatching (Table A3.2), which in the case of *C. chloris* was influenced by year, with 2012 having lower hatching probabilities relative to 2010 (GLMM, Chi-squared = 10.795, p = 0.006; Fig. 1). In all cases, except for *C. chloris*, the probability of hatching was higher than that of egg laying (Fig. 1). The probability of success of nests containing nestlings was relatively high for all species (from 70% in *C. chloris* to 91% in *S. serinus*) and was not affected by the presence of herbaceous cover (Fig. 1). In the case of *L. cannabina* the model for the probability of fledging could not be calculated because of insufficient sampling size (22 nests with chicks, 17 of which showed evidence of fledging).

**DISCUSSION**

Soil management regimes influenced nest densities of songbirds in conventional olive groves of southern Spain, but the effects were species-specific for the three most abundant cardueline finches. Contrary to our expectations, the implementation of herbaceous cover did not seem to affect the overall breeding success of these songbird species, nor any of the stages of their breeding cycle. Our study shows a higher nest loss rate during egg laying and the hatching period, indicating that early stages of the breeding cycle are generally more sensitive.

Nest densities in olive groves with and without herbaceous cover differed for the three species of cardueline finches. Nest densities of *Chloris chloris* were higher in olive groves with herbaceous cover, while nest densities of *Serinus serinus* were higher in olive groves without herbaceous cover, and nest densities of *Linaria cannabina* did not differ between soil management regimes. These patterns are consistent with previous studies in the same olive groves that reported higher abundance of greenfinches in olive groves with herbaceous cover, while serins were more abundant in olive groves without herbaceous cover (Castro-Caro et al. 2014a). The observed differences in nest densities could be related to the species-specific nestlings’ diet (Gil-Delgado et al. 2009). Herbaceous cover can provide a diverse source of food items including a wide range of seeds and arthropods (Wilson et al. 1999, Vickery et al. 2009). For example, Carpio et al. (2019) found that herbaceous cover increases arthropod abundance and diversity in olive groves, which would benefit nestlings with generalist diets, like greenfinches (Valera et al. 2005). Future studies should consider the availability of different food sources provided by herbaceous cover for bird species with different degrees of diet specialization.

Even if we used a naïve estimate that tends to overestimate breeding success (Jehle et al. 2004), the overall breeding success of songbirds found in the present study (19% for *L. cannabina*, 16% for *C. chloris*, and 38% for *S. serinus*) was low compared to nest survival rates reported in natural (59%; Lu 2005) or urban (50%; Ludvig et al. 1995) habitats, or in other agro-ecosystems (47%; Morgan et al. 2010, 66%; McLeod et al. 2004). However, the rates of breeding success in the present study are comparable to those documented for some species in intensive agro-ecosystems (11% for skylarks *Alauda arvensis* in conventionally managed cereal fields; Wilson et al. 1997, 10% to 38.9% for songbirds in vineyard orchards of Northern Italy; Assandri et al. 2017). These low nest success rates are generally attributed to
predation (Evans 2004, Castro-Caro et al. 2014b). In our study, 56.6% of nest failures (314 out of 555 failed nests) could be unequivocally attributed to predation, as attested by clear signs of predation (Fig. A2.1). Our estimates of predation rates are likely underestimates, as cases where predators remove whole eggs would have remained undetected.

There were differences in the probabilities of transition between the different stages of the reproductive cycle for the three species. Nest survival rate was generally lower in the stage of egg-laying and hatching compared to fledging. We found a relatively high number of nests initiated but abandoned before egg-laying (43.4%, 241 out of 555 failed nests). The reason for failure of these nests with no signs of predation could be reasonably attributed to nest disturbance. Management activities can be an important driver in nest desertion at early stages (Barber et al. 2010, Bretagnolle et al. 2018). Assandri et al. (2017) found that in vineyards, 51% of nests were abandoned before egg-laying, and the probability of early abandonment was positively related to the amount of access to the fields that farmers had for management activities. In the breeding season, olive groves are subjected to several management practices that entail the use of heavy machinery and agrochemicals to control weeds (ploughing and/or spraying herbicides) and the spraying of insecticides and fertilizers to the tree canopies.

This study also suggests that interannual variation in weather conditions may be an important constraint on nesting success of cardueline finches in olive groves. We found a significant effect of year for the probability of egg laying in *S. serinus* and the probability of hatching for *C. chloris*, with lower values in 2012 compared to other years. In the Mediterranean region average precipitation is 550 mm, which is concentrated mainly between November and April and characterized by an irregular distribution (Aparicio 2008). In 2012, the breeding season started with a severe drought (rainfall in January was 14 mm, whereas for the same period in 2010 and 2011, rainfall was 360 and 156 mm, respectively). The lack of rainfall at the beginning of the breeding season in 2012 may have led to poorer growing conditions that had a stronger effect on breeding success than the presence of herbaceous cover.

There is an ongoing debate about whether agro-environmental management practices mainly benefit common species or if their effects favor rare and declining species (Sicurella et al. 2018). Castro-Caro et al. (2014a, 2015) showed that, in olive groves in southern Spain, the presence of herbaceous cover and hedges had a positive effect on two birds with unfavorable conservation status (BirdLife International 2004), the Rufous-tailed Scrub-Robin *Cercotrichas galactotes* and the Woodchat Shrike *Lanius senator*, classified respectively as endangered (EN) and Vulnerable (VU) in Spain (Madroño et al. 2004). In the present study 45 out of 46 nests of *Lanius senator* were located in groves with ground cover (Table 1), supporting the idea that the implementation of agricultural practices that increase structural complexity like promoting herbaceous cover in conventional olive groves could be beneficial for species of conservation concern.

In conclusion, our study shows that conventional olive groves in general, irrespective of the soil management system, might not be a suitable habitat for bird reproduction. The low breeding success we found suggests that nest predation could be important drivers of the declines in farmland birds. The isolation of the few groves with herbaceous cover in the matrix of conventional groves with bare ground could lead to a dilution of the potential benefits of this management practice (Hole et al. 2005). Our study compared olive groves with and without herbaceous cover; future studies should consider more nuanced aspects of herbaceous cover, including the amount of plant cover, vegetation height, and the composition of the herbaceous cover. Further, studies documenting the responses of predator communities to spatial and temporal heterogeneity in resources, e.g., nests, in landscapes with different degrees of intensification as well as the consequences of nest disturbance due to management activities on nest desertion are needed to design effective measures to promote biodiversity in Mediterranean farmland systems.

**Responses to this article can be read online at:**
https://www.ace-eco.org/issues/responses.php/2038

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**Fig. A1.1.** Image of olive groves in early Spring with (A) and without (B) herbaceous cover. In olive groves with herbaceous cover the area below the tree crowns is kept plant-free by the application of contact and systemic herbicides. Herbaceous cover is mown in late Spring to avoid water competition.
Fig. A2.1. Signs recorded during nest monitoring include evidence of nest predation (A, B) or nest success. A) Serin (*Serinus serinus*) nest showing signs of disturbance. B) Linnet (*Linaria cannabina*) with eggs predated by rodents, as indicated by the teeth marks on egg shells. C) Nest success was evidenced by the presence of bird faeces on nest edges.
Table A3.1. Model results for nest densities for the most common breeding songbirds in olive groves of southern Spain: *Linaria cannabina*, *Chloris chloris* and *Serinus serinus*. Linear models including the effect of herbaceous cover and year were used.

| Species                | Effect | F-value | p-value |
|------------------------|--------|---------|---------|
| *Linaria cannabina*    | cover  | 2.821   | 0.104   |
|                        | year   | 0.052   | 0.950   |
| *Chloris chloris*      | cover  | 8.617   | 0.007   |
|                        | year   | 1.298   | 0.289   |
| *Serinus serinus*      | cover  | 9.640   | 0.004   |
|                        | year   | 0.200   | 0.820   |
Table A3.2. Model results for the overall breeding success and the transition probabilities between different stages of the breeding cycle for all bird species, and for the most common breeding songbirds in olive groves of southern Spain: *Linaria cannabina*, *Chloris chloris* and *Serinus serinus*. Generalized Linear Models including site as random effect and the effect of herbaceous cover and year as fixed effects were used.

|                       |     |     |
|-----------------------|-----|-----|
| **a. all birds**      |     |     |
| Breeding success      | cover| 1.098 | 0.295 |
|                       | year | 4.001 | 0.135 |
| Breeding              | cover| 1.124 | 0.289 |
|                       | year | 3.363 | 0.186 |
| Hatching              | cover| 6.827 | 0.009 |
|                       | year | 10.795 | 0.005 |
| Fledging              | cover| 0.003 | 0.959 |
|                       | year | 3.139 | 0.208 |
| **b. Linnaria cannabina** | |     |
| Breeding success      | cover| 1.271 | 0.26  |
|                       | year | 1.694 | 0.193 |
| Breeding              | cover| 2.426 | 0.119 |
|                       | year | 5.497 | 0.064 |
| Hatching              | cover| 2.028 | 0.154 |
|                       | year | 3.873 | 0.144 |
| Fledging              | model failed to converge | | |
| **c. Chloris chloris** | |     |
| Breeding success      | cover| 0.393 | 0.822 |
|                       | year | 4.773 | 0.189 |
| Breeding              | cover| 3.425 | 0.064 |
|                       | year | 1.980 | 0.372 |
| Hatching              | cover| 0.283 | 0.595 |
|                       | year | 10.245 | 0.006 |
| Fledging              | cover| 0.063 | 0.802 |
|                       | year | 2.606 | 0.272 |
| **d. Serinus serinus** | |     |
| Breeding success      | cover| 0.615 | 0.433 |
|                       | year | 3.268 | 0.195 |
| Breeding              | cover| 0.728 | 0.394 |
|                       | year | 6.618 | 0.037 |
| Hatching              | cover| 0.199 | 0.655 |
|                       | year | 2.192 | 0.334 |
| Fledging              | cover| 2.328 | 0.127 |
|                       | year | 1.983 | 0.371 |