University of Groningen

Breeding biology of Western Bonelli's Warblers *Phylloscopus bonelli* in the Mediterranean region

Roncalli, Gianluca; Diego Ibanez-Alamo, Juan; Soler, Manuel

Published in:
Bird Study

DOI:
[10.1080/00063657.2016.1215408](https://doi.org/10.1080/00063657.2016.1215408)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2016

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Roncalli, G., Diego Ibanez-Alamo, J., & Soler, M. (2016). Breeding biology of Western Bonelli's Warblers *Phylloscopus bonelli* in the Mediterranean region. *Bird Study*, 63(3), 413-424.
<https://doi.org/10.1080/00063657.2016.1215408>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Breeding biology of Western Bonelli's Warblers *Phylloscopus bonelli* in the Mediterranean region

Gianluca Roncalli, Juan Diego Ibáñez-Álamo & Manuel Soler

To cite this article: Gianluca Roncalli, Juan Diego Ibáñez-Álamo & Manuel Soler (2016) Breeding biology of Western Bonelli's Warblers *Phylloscopus bonelli* in the Mediterranean region, Bird Study, 63:3, 413-424, DOI: [10.1080/00063657.2016.1215408](https://doi.org/10.1080/00063657.2016.1215408)

To link to this article: <https://doi.org/10.1080/00063657.2016.1215408>

Published online: 15 Aug 2016.

Submit your article to this journal [↗](#)

Article views: 82

View Crossmark data [↗](#)

Citing articles: 1 View citing articles [↗](#)

Breeding biology of Western Bonelli's Warblers *Phylloscopus bonelli* in the Mediterranean region

Gianluca Roncalli^a, Juan Diego Ibáñez-Álamo^{b,c} and Manuel Soler^a

^aDepartamento de Zoología. Facultad de Ciencias, Universidad de Granada, Granada, Spain; ^bAnimal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands; ^cDepartment Wetland Ecology, Estación Biológica de Doñana, CSIC, Sevilla, Spain

ABSTRACT

Capsule: The Western Bonelli's Warbler *Phylloscopus bonelli* has a nest success of only 25% in the core of its range in western Europe.

Aims: To investigate the breeding biology of Western Bonelli's Warbler *P. bonelli*, focusing on possible altitude effects and potential reproductive problems.

Methods: Three Western Bonelli's Warbler populations were monitored during the 2012 and 2013 breeding seasons in the massif range of Sierra Nevada, Spain. We determined all the breeding parameters and calculated daily survival and success rates for each reproductive period.

Results: The three studied populations did not differ in any breeding parameters. Altitude showed a positive relationship with clutch size and duration of incubation period, but a negative relationship with nestling tarsus growth and body mass gain. Daily survival rates during incubation and nestling periods were similar to those of common warblers, but the species presented a low breeding success of 25%.

Conclusion: The absence of differences among the three populations suggests that the information provided here could be representative of its distribution in the woodlands of Sierra Nevada. The novel and detailed information reported is crucial not only for expanding our understanding of this species but also to draw attention to the potential risks that it might face in the near future, considering the reduction that this species has suffered in Sierra Nevada during recent decades.

ARTICLE HISTORY

Received 5 November 2015

Accepted 17 May 2016

The study of the breeding parameters of a species is essential for the understanding of its biology and ecology, but this information is even more important for those species which are poorly known or threatened (Green 2004). The Western Bonelli's Warbler *Phylloscopus bonelli* (hereafter Bonelli's Warbler) is one such poorly known species (Clement & Christie 2013). To date, the few studies about this species focused on other topics (i.e. genetics, acoustics or migration/distribution range) rather than on the breeding biology itself (Helbig *et al.* 1995, Bremond 1976, Prince *et al.* 1997, Dietzen *et al.* 2007, Pilastro *et al.* 2008). In contrast to other European *Phylloscopus* species whose breeding biology has been well studied (e.g. Wood Warbler *Phylloscopus sibilatrix*, Chiffchaff *Phylloscopus collybita* and Willow Warbler *Phylloscopus trochilus*; see Clement & Christie 2013), there is only a single detailed study about the breeding biology of Bonelli's Warblers (Riedinger 1974). This study was carried out more than 40 years ago and investigated a lowland population in southern Germany. Bonelli's

Warblers typically inhabit more southerly regions and higher altitudes, such as the mountain ranges of the western Mediterranean (Clement & Christie 2013). Thus, it is likely that the reproductive parameters reported in by Riedinger (1974), based on a peripheral population and different latitudinal and altitudinal ranges, do not fully represent the breeding biology of the species. In fact, animal populations living on the edge of their distribution ranges usually present variations in some life-history traits in order to cope with the environmental challenges of such areas (Diaz *et al.* 2007). Latitude and altitude can also affect life-history traits (Badyaev 1997, Badyaev & Ghalambor 2001, Cardillo 2002). For example, several within and between species studies have demonstrated that clutch size increases with latitude because of the seasonality of resources (i.e. high food availability per individual bird in spring; Bell 1996, Yom-Tov & Geffen 2011) or a shorter duration of the breeding season in temperate areas compared to the tropics (Skutch 1985, Schaefer *et al.* 2004). On the other hand, the ecological

conditions at high altitudes, such as colder temperatures, shorter breeding seasons and greater fluctuations in food availability, favour an increased investment per offspring (i.e. larger eggs; Badyaev 1997, Lu *et al.* 2009, Li & Lu 2012). Riedinger (1974) supplied basic information regarding some aspects of the breeding biology of Bonelli's Warbler, such as clutch size, laying date and egg parameters, but did not provide other key data such as daily survival rates or hatching/fledging success rates, nestling growth rates or parental activity. To our knowledge, no previous studies have provided detailed information on the breeding biology of Bonelli's Warblers in its core habitat; the mountain woodlands of the Mediterranean.

The conservation status of Bonelli's Warblers is of 'Least Concern' according to the International Union for Conservation of Nature (BirdLife International 2014), however it holds the 'SPEC 2' category according to the directive of the European Union on Birdlife, which categorized this species with an unfavourable conservation status in Europe (Birdlife International 2004). This matter raises some concerns about the viability of its populations considering that the majority of Bonelli's Warblers breed in Europe. For instance, populations from southern Germany (Del Hoyo *et al.* 2006) and France (Dubois *et al.* 2000; Eionet 2014) have been in decline both in population size and breeding range. In Spain, where 65% of all individuals are present (Del Hoyo *et al.* 2006), Bonelli's Warblers have been experiencing a moderate increase (Sociedad Española de Ornitología; SEO/BirdLife 2010), but in some areas, such as the southern parts of the Iberian Peninsula, they are in serious decline (Zamora & Barea-Azcón 2015). In fact, Bonelli's Warblers are considered of 'special interest' in Spain, where the loss of habitat due to frequent fires, human land-use changes and the impact of grazing by livestock could explain their local population declines (Urios *et al.* 1991, Valle 2003).

The main aim of this study is to investigate the breeding biology of the Bonelli's Warbler in the core of its distribution range; the woodlands of Sierra Nevada (southeast Spain). This species has been one of the most abundant passerine birds in that area (Martinez *et al.* 2010), but has suffered an important reduction in breeding population size (from 1.36 birds per hectare to 0.34 birds per hectare) in the last 30 years (Zamora & Barea-Azcón 2015). In addition, we provide new key data such as hatching and fledging success, and breeding behaviour such as nest building and incubation from video recordings. It is important to know this information as it is so far undocumented,

but it would also help to diagnose and address the drivers of the population declines.

Material and methods

Study area and population

Bonelli's Warblers were monitored during the breeding seasons of 2012 and 2013, from the end of April to mid-July, in the National Park located in the Sierra Nevada high massif in southeast Spain (37°N 3°W). Bonelli's Warbler breed in mountain woodlands, principally composed of Pyrenean Oak *Quercus pirenaica*, located in the supramediterranean climatic belt. These areas have high values of species richness, diversity and density in the massifs of south Spain (Martinez *et al.* 2010). The climate is characterized by an irregular annual rainfall, ranging between 650 and 1200 mm per year, depending mostly on altitude. The average temperatures vary between 8°C and 13°C, descending frequently below 0°C during winter and reaching up to 20°C in summer (Rivas-Martínez 1987). During the first year, three areas with similar altitudinal ranges were investigated: the Serpentina area (37°08'N 3°24'W), between 1000 and 1600 m above sea level (a.s.l.), the Monachil area (36°05'N 3°26'W), between 1200 and 1900 m a.s.l. and the Soportújar area (36°56'N 3°23'W), between 1200 and 2000 m a.s.l. We chose these three areas on the basis of a previous study (Martínez *et al.* 2010) in which distribution and density of Bonelli's Warblers and other species living in Sierra Nevada were monitored. Because of the high density of breeding pairs reached in these three areas (1.10, 0.93 and 0.92 pairs per hectare for Serpentina, Monachil and Soportújar, respectively; Martínez *et al.* 2010), we think that the three studied populations should show typical reproductive parameters for the woodlands of the Mediterranean region at the core of its distribution. The studied populations also offered a large altitudinal gradient (around 1000 m) allowing us to test the potential effect of this factor on the breeding biology of this species. The study populations were on average 13.6 km from each other (range: 6–20 km) and were located on both north (Serpentina and Monachil) and south (Soportújar) facing slopes. During 2013 we concentrated our research effort only in the Soportújar area.

The three areas have steep slopes and open, warm deciduous woodland composed of Pyrenean Oak, a deciduous tree which is distributed from southwest France through to north Morocco. In the southern Iberian Peninsula it grows between 1000 and 1800 m a.s.l., occasionally as high as 1900 m a.s.l. on south

facing slopes, in siliceous soils, mostly in the supramediterranean climatic belt (Costa-Tenorio *et al.* 1998). Holm Oak *Quercus ilex* and different species of pines, *Pinus pinaster*, *Pinus Nigra* and *Pinus sylvestris* are the other common tree species widespread in the most elevated part of the study area. The undergrowth is dominated by bushy areas with legumes, such as brooms (*Cytisus scoparius*, *Adenoarbus decorticans*) and some open grassy areas (Costa-Tenorio *et al.* 1998). In this habitat, Bonelli's Warblers forage principally on insects, such as small flies and mosquitoes (Diptera), aphids (Aphidoidea) or small caterpillars (Lepidoptera), but also take small spiders (Araneae) and other invertebrates (Cramp 1985).

Data collection

We located nests by following parental activity. Initially we concentrated on male songs in order to detect territories, and subsequently we looked for females for periods of 30 minutes per day. If the female was not detected on the first day, we visited the territory on subsequent days to find her and locate the nest (always limited to 30 minutes periods of searching to reduce risk of desertion). When we found a nest we marked its exact location and altitude with a Global Positioning System device (Garmin Geko 201). Each nest was visited every 2–3 days in order to obtain the following biological parameters: clutch size, laying date, hatching date, incubation period, brood size, hatching success, nestling period, number of nestlings that left the nest, fledging success and breeding success. See below for definition of each parameter. Given that the Bonelli's Warbler is a single brooded species (Cramp 1985, own data), we calculated each parameter for each pair.

Laying and incubation stages

Laying date was the day on which the female laid the first egg (day 1 = 1 April). Since Bonelli's Warblers usually start incubating with the last egg (Cramp 1985), the incubation period was calculated as the period between the laying of the last egg and the date on which the first egg hatched (hatching date).

In order to study incubation behaviour, we captured the adults (at least one of the pair) using mist nets, and filmed the nests to collect data on adults' activity during this period. All individuals were measured and ringed with colour ring combinations that allowed for individual recognition from a distance (by using binoculars) or in the video recordings. We captured 33 individuals: 23 males, 7 females and 3 individuals for which we could not determinate the sex. We determined the sex by using brood patch or body

measures (weight, tarsus and wing length) as, in the *Phylloscopus* genus, males are slightly larger than females (Tiainen 1982). We confirmed all the data by analysing the video recordings in which we could recognize the ringed birds and the different breeding behaviour patterns between males, which never entered into the nest, and females. Nests were recorded for two hours between 08:00 and 13:00 hours, one or two days after the start of incubation using a Panasonic HDC-SD40 video camera placed within 3 m of the nest. We analysed the videos using VLC software and extracted the following variables: (i) females' incubating time (time spent incubating by females per hour); (ii) nest visits (number of female visits to the nest for incubating); (iii) off-bouts (time in which females was away from the nest per hour). The placement of cameras did not seem to affect the behaviour of birds (pers. obs.) and no nest was deserted because of the presence of the camera.

We calculated the daily survival rate for the incubation period (Johnson 1979). This method considers both the fate of the nest and the known activity period, correcting for the increased probability of a nest surviving to later stages. Therefore, in this procedure the daily survival rate indicates the probability that a nest with eggs will survive to the next day. In addition, we provided the proportion of nests in which at least one egg hatched (hatching success).

Brood size refers to the number of eggs that successfully hatched. When the clutch was completed, we measured length and width of all eggs with a digital calliper (accuracy 0.01 mm), and weighed them with a digital balance (accuracy 0.1 g) just after clutch completion. The volume of the eggs was calculated with the following formula: $0.51 \times \text{length} \times \text{wide}^2$ (Hoyt 1979).

Nestling period

Nestling period was calculated as the period between the hatching of the first egg and the date in which nestlings fledged (i.e. the first day we found the nest empty). Nestlings are able to leave the nest when 11 days old (Del Hoyo *et al.* 2006), so all nests found empty before this time were considered to have had their contents predated. We calculated the daily survival rate for the nestling period and the complete breeding period using the procedure described above. We also calculated the proportion of nests in which at least one nestling fledged from successfully hatched nests (fledging success). The number of fledglings was calculated as the number of nestlings per nest that successfully left the nest. Finally, we calculated the daily survival rate considering the whole breeding period, from laying to the date of the fledging. We also calculated the

proportion of nests in which at least one nestling fledged considering all the nests found during the breeding season (breeding success). Nests in which at least one nestling was found dead or disappeared during the nestling period were considered to have suffered starvation because potential nest predators in the study area, such as Jay *Garrulus glandarius*, Montpellier Snake *Malpolon monspessulanus*, rats *Rattus* sp. and domestic cats *Felis silvestris catus* are large enough to ingest all the nestlings at the same time. Body mass, tarsus and wing length of every nestling were measured three times along the nestling period when they were 2–4, 5–7 and 8–10 days old. In every visit we marked each nestling of the brood with a different colour by means of non-toxic markers (FaberCastel Multimark) to allow for individual differentiation in subsequent visits.

Statistical analysis

All analyses were performed using R 2.15.3 for Windows (R Development Core Team 2012). We used ANOVA and Kruskal–Wallis tests to look for differences in breeding parameters among the three study areas during 2012. We used ANOVA to analyse laying date, while Kruskal–Wallis tests were used to analyse clutch size, incubation, number of eggs hatched, duration of nestling period and number of nestlings fledged because of the non-normal distribution of the dependent variable. Finally, we used Fisher exact tests to analyse the frequency of hatching and nestling success. The study area was considered as a factor. After confirming that there were no significant differences between the three areas for any of the variables considered (see results), we decided to use a single database combining all data collected as representative of the population of Sierra Nevada.

We fitted linear models (LM, package stats in R) considering all the predictors that could be biologically relevant to each of the breeding parameters (laying date, clutch size, incubation period, brood size, nestling period, altitude and year). When two predictors presented collinearity we decided to drop the one which could be linearly predicted from the other. For instance, between brood size and clutch size, we considered only brood size which indirectly predicted clutch size. Using this procedure we presented the models with all possible biological predictors for each dependent variable, showing both significant and non significant ones. For all LM models we considered altitude as a covariate and year as a fixed effect because we were interested in looking for an altitudinal effect and the potential differences between those two years.

Additionally we had only two years of data and therefore we could not consider year as a random factor (Zuur et al. 2009).

To calculate if the proportions of hatched eggs with respect to clutch size, fledged chicks with respect to the brood size and fledged chicks with respect to the clutch size were related to year or to altitude we fitted χ^2 test and a generalized linear model (GLM) respectively.

In order to analyze egg size and mass, we used a linear mixed model (LMM, package nlme in R) in which we included nest as random effect to control for non-independence of eggs from the same nest.

We calculated nestling growth in terms of mean daily gain in body mass, tarsus length and wing length, by assuming that the growth was linear for most of the nestling period and by fitting a linear slope through the parameters against age for each nestling. We fitted a LMM model in which we considered the slope of each variable as the response variables and brood size, nestling period, altitude and year as predictors, while nest was considered as a random factor in order to control for non-independence of nestlings from the same nest.

At the end of all model analyses we visually inspected residuals and residual *versus* fitted values to check for deviations from normality using qqplot. All means are given with $\pm$ se.

Results

We found 40 and 76 nests in 2012 and 2013, respectively, located between 1283 and 1888 m a.s.l.

Figure 1. Regression of the time between the end of nest building and the laying of the first egg, and the laying date of each nest. Dates are calculated in days after 1 April. As the season progressed the time between nest building and laying was reduced.

Table 1. Breeding parameters of Western Bonelli's Warblers *Phylloscopus bonelli* in three study areas in 2012. Statistical tests comparing sites were: ANOVA (laying date), Kruskal–Wallis (clutch size, incubation, eggs hatched, nestling period and chicks fledged) and Fisher's exact test (frequency of hatching and nestling success).

Parameters				Soportujar			Monachil			Serpentina		
Incubation period	Test statistic (<i>F</i> or <i>H</i>)	df	<i>P</i> value	Mean	se	<i>N</i>	Mean	se	<i>N</i>	Mean	se	<i>N</i>
Laying date	0.22	2	0.81	30 May	4.24	11	27 May	2.56	13	27 May	5.34	9
Clutch size	2.39	2	0.30	4.62	0.26	7	4.75	0.13	12	4.29	0.29	7
Incubation	2.45	2	0.29	12.25	0.16	8	12.57	0.43	7	11.75	0.25	4
Eggs hatched	3.07	2	0.22	4.50	0.5	6	4.57	0.2	8	3.50	0.5	4
Hatching success			0.58	62%		8	64%		11	33%		6
<i>Nestling period</i>				<i>Mean</i>	<i>se</i>	<i>N</i>	<i>Mean</i>	<i>se</i>	<i>N</i>	<i>Mean</i>	<i>se</i>	<i>N</i>
Nestling period	0.37	2	0.83	12.0	0.23	6	12.5	0.64	4	13.0	2.0	2
Chicks fledged	0.14	1	0.71	4.0	0.58	4	4.3	0.33	3	-	-	-
Nestling success			0.75	50%		8	33%		9	33%		6

(average 1654 ± 13 m, $n = 93$). The nests were found during nest building and egg laying periods, when females typically give excitement calls when coming to the nest (Cramp 1985). We did not detect significant differences for any of the breeding parameters considered among the three different study areas in 2012 (all $P > 0.05$, Table 1).

Nest building stage

The time between the end of nest building and the laying of the first egg decreased as the breeding season advanced (LM, $F_{1,36} = 6.32$, $P = 0.02$, Figure 1). Two out of 14 nests and 12 out of 27 found during the nest building periods in 2012 and 2013, respectively, were either not finished or finally unused by Bonelli's warblers. Of these 12 nests, 10 were abandoned in the first part of the breeding season (before June). All nests found were built exclusively by females. Once the place was chosen she started to set the natural hollow (sometimes made by the bird) and later she positioned some leaves in it. Finally, she placed grass to cover the nest. Both leaves and grass were collected from the surroundings of the nest site, sometimes more than 20–30 m away from it.

Laying and incubation stages

Laying date

Eggs were laid earlier in 2013 (mean = 20 May $\pm$ 2 days; $n = 42$, range = 7 May–27 June) than in 2012 (mean = 29

May $\pm$ 2 days, $n = 26$, range = 15 May–22 June; $F_{1,58} = 13.45$, $P < 0.01$), while we did not find significant differences depending on altitude considering both years together ($F_{1,58} = 0.45$, $P = 0.50$). Bonelli's Warbler females in our populations laid a mean of 4.90 ± 0.08 eggs ($N = 71$, median = 5, range = 3–6, Table 3).

Clutch size

A significant negative relationship between clutch size and laying date (Figure 2) was found in the model (LM, $F_{1,47} = 46.82$, $P < 0.01$, $y = -0.038x + 6.80$, Table 2). This implies that females breeding earlier laid more eggs than females breeding later in the season. Moreover, we found that clutch size increased with altitude (LM, $F_{1,47} = 11.79$, $P < 0.01$, Table 2).

Figure 2. Regression between clutch size and laying date. Dates are calculated in days after 1 April. Females laid fewer eggs as the breeding season advanced.

Table 3. Distribution of clutch sizes in Western Bonelli's Warbler *P. bonelli* populations from southern Spain and southern Germany. Clutches were significantly larger in Germany ($F_{1,125} = 12.33$, $P < 0.001$).

Clutch size	3 (%)	4 (%)	5 (%)	6 (%)	7 (%)	Mean	
Spain	4	17	63	15	0	4.9	$N = 71$
Germany	0	5	64	25	5	5.3	$N = 56$

Table 2. Summary of linear mixed models exploring the variation in the breeding parameters of Western Bonelli's Warblers *P. bonelli*. Coefficients of the models (β) show positive or negative relationships between predictors and dependent variables for significant relationships.

	β	df	F	P value
<i>Laying date</i>				
Altitude		1	0.45	0.50
Year	-1.145	1	13.45	0.001
Residuals		58		
<i>Clutch size</i>				
Laying date	-0.039	1	46.82	<0.001
Altitude	+0.002	1	11.79	0.001
Year		1	0.08	0.77
Residuals		47		
<i>Incubation period</i>				
Clutch size		1	0.21	0.65
Laying date		1	3.19	0.09
Altitude	+0.004	1	8.24	0.007
Year		1	2.61	0.11
Residuals		28		
<i>Brood size</i>				
Incubation period	-0.636	11	21.06	< 0.001
Clutch size	+1.488	1	18.99	<0.001
Laying date		1	1.87	0.18
Altitude		1	0.26	0.61
Year		1	0.13	0.71
Residuals		21		
<i>Nestling period</i>				
Brood size		1	0.19	0.73
Laying date		1	0.42	0.52
Altitude		1	0.17	0.68
Year		1	0.32	0.57
Residuals		13		
<i>Number of chicks fledged</i>				
Nestling period		1	0.44	0.52
Brood size	+2.220	1	14.80	0.005
Laying date		1	0.07	0.79
Altitude		1	0.38	0.55
Year		1	0.21	0.65
Residuals		10		

Incubation period

The incubation period was 12.62 ± 0.16 days (range = 11–15; $N = 37$), and it was not correlated with clutch size (LM, $F_{1,28} = 0.21$, $P = 0.65$) but increased with altitude (LM, $F_{1,28} = 8.24$, $P < 0.01$, Table 2). The mean

time spent incubating per hour was 45.39 ± 4.15 minutes ($N = 9$). Females left the nest a mean of 1.28 ± 0.12 times per hour ($N = 9$) and spent a mean of 10.03 ± 0.83 minutes out of the nest per hour ($N = 9$). We observed only once a visit of a male warbler that arrived to the nest with a grasshopper in the bill and fed it to the incubating female.

Eggs size

Mean egg sizes were: 15.16 ± 0.08 mm in length (range = 13.95–17.01 mm, $N = 65$) and 12.22 ± 0.06 mm in width (range = 10.93–15.81 mm, $N = 65$). The mean egg volume and mass were 1158.86 ± 13.52 mm³ and 1.11 ± 0.01 g ($N = 65$), respectively. Both egg volume and mass decreased in larger clutches (LMM, $F_{1,44} = 15.26$, $P < 0.01$, $F_{1,44} = 11.17$, $P < 0.01$, respectively, Figure 3). Although the relationship did not reach the statistically significant threshold, egg volume tended to decrease with altitude (LMM, $F_{1,44} = 3.60$, $P = 0.06$) independently of the clutch size (LMM, $F_{1,44} = 0.42$, $P = 0.52$). Egg mass was not correlated with altitude (LMM, $F_{1,44} = 0.45$, $P = 0.49$).

Daily survival rate for incubation period and hatching success

Daily survival rate for the incubation period was 0.958 ($N = 70$). The proportion of nests in which at least one egg hatched did not vary between years or altitude ($\chi^2 = 1.52$, $df = 1$, $P = 0.22$, and GLM $z = 1.17$, $P = 0.24$, respectively). In our study population a mean of 4.5 ± 0.17 ($N = 34$) eggs hatched per nest (brood size). A greater proportion of eggs hatched in larger clutches than in smaller clutches (LM model, $F_{1,21} = 18.99$, $P < 0.01$, Table 2). Moreover, we found a negative relationship between brood size and incubation period (LM model, $F_{1,21} = 21.06$, $P < 0.01$, Table 2).

Nestling stage

Nestling period

Nestlings remained in the nest for 12.5 ± 0.22 days (range = 11–15; $N = 24$). The nestling period was not associated with any parameters in the minimal model (Table 2).

Daily survival rate for nestling period and fledging success

The daily survival rate for nestling period was 0.945 ($N = 45$). The proportion of nests in which at least one nestling fledged over successfully hatched nests did not differ between years ($\chi^2 = 1.44$, $df = 1$, $P = 0.23$) or along altitude (GLM $z = 1.63$, $P = 0.09$). Successful pairs managed to fledge a mean of 4.00 ± 0.24 nestlings

Figure 3. Relationship between clutch size and (a) egg mass and (b) egg volume. Eggs in larger clutches were smaller and lighter.

($N = 18$). This value was only significantly correlated with brood size (LM, $F_{1,8} = 14.80$, $P < 0.01$, Table 2).

Nestling growth

Nestling growth was estimated from the linear slope of body mass, tarsus length and wing length against age for each nestling. Growth of tarsus was significantly and negatively correlated with the duration of the nestling period ($F_{1,26} = 9.36$, $P = 0.02$); body mass gain was only marginally non-significantly related to the duration of the nestling period ($F_{1,26} = 4.98$, $P = 0.06$) and wing length growth did not show any relationship with the length of the nestling period ($F_{1,26} = 0.17$, $P = 0.68$). Nestling growth was not correlated with brood size (mass: $F_{1,26} = 0.14$, $P = 0.72$; tarsus length: $F_{1,26} = 3.86$, $P = 0.10$; wing length: $F_{1,26} = 0.44$, $P = 0.53$). Nestling development was significantly and negatively correlated with altitude for growth of body mass and tarsus length ($F_{1,26} = 12.34$, $P = 0.01$; $F_{1,26} = 28.10$, $P < 0.01$, respectively) but not for wing length ($F_{1,26} = 0.02$, $P = 0.92$).

Daily survival rate for breeding period and breeding success

Nestling starvation was found in four nests (17%, $N = 23$) in 2012 and in six nests in 2013 (12%, $N = 51$) and did not vary significantly between years ($\chi^2 = 0.43$, $df = 1$, $P = 0.51$). The daily survival rate for the breeding period was 0.955 ($N = 79$). The proportion of nests in which at least one nestling fledged did not differ significantly between 2012 and 2013 ($\chi^2 = 1.60$, $df = 1$, $P = 0.21$) nor in relation to altitude (GLM $z = 0.38$, $P = 0.70$).

Discussion

The absence of differences in breeding parameters among Bonelli's Warblers from all three study areas for 2012 suggests that our findings could be considered as representative of its distribution in the mountain woodlands of Sierra Nevada.

Nest building stage

All nests in our study were located above 1200 m a.s.l., which is much higher than other European populations, where nests can be found as low as 300 m a.s.l. (Riedinger 1974, Cramp 1985). This can be explained because the environmental requirements for breeding in this species (i.e. humidity and temperature) at these altitudes in Mediterranean areas correspond to those of lower altitudes further north (Waught 2002). Furthermore, our data suggest that the Bonelli's

Warbler is the highest breeding *Phylloscopus* species in Europe (Cramp 1992).

All nests were located on the ground, a trait common to all species of the genus *Phylloscopus* (Cramp 1985). However, for some species there is variation in this trait. For example, in the Willow Warbler about 7% of nests were recorded as being more than 30 cm above the ground (Cramp 1955) and in the Chiffchaff more than 10% of nests were found at 50 cm above the ground (Rodrigues & Crick 1997). In contrast, for the Bonelli's Warbler, we found that all (100%) nests were placed on the ground, as observed in a German population (Riedinger 1974), which suggests that this is a fixed trait for this species throughout its distribution area. Nests were a domed structure located in small hollows. They were usually located under overhanging tussocks or at the base of Spanish Broom *Spartium junceum* plants and sometimes under overhanging banks.

Constant monitoring of nests allowed us to get information about nest building behaviour. As occurs in other populations of Central Europe (Cramp 1985), we found that Bonelli's Warbler nests were built exclusively by females. During the first part of the breeding period females built the nest and waited for more than 10 days before laying; while as the season progressed the time between nest building and laying was reduced (Figure 1). In contrast, in a German population (Riedinger 1974) no more than 3–4 days elapsed between the end of the nest building stage and the start of laying. This long delay in laying has also been found for other *Phylloscopus* species (e.g. Wood Warbler *P. sibilatrix*; Wesolowski & Maziarz 2009). Probably the females that arrived first built their nests earlier, but delayed the date of laying because food abundance could be relatively low at the beginning of the breeding season, when overnight temperatures are still frequently below zero (Stutchbury & Robertson 1987, Wesolowski & Maziarz 2009). It has also been suggested that early settling females delay the laying of their eggs in order to benefit from breeding synchronously with other conspecifics through the dilution of predation risks (Stutchbury & Robertson 1987, Maddox & Weatherhead 2006, Wesolowski 2013).

We recorded 14% and 21% nest abandonment during nest building in 2012 and 2013, respectively. Several reasons could be behind this result. It is possible that our presence in the field provoked these abandonments, however, we think that it is highly unlikely given that our activity at the nest was not intensive (one visit every 2–3 days, and only 30 minutes of nest searching per day from a considerable distance before finding the nest location). Nest

desertion could also be due to mate switching or predation of eggs laid between nests visits (Westneat 1992, Maddox & Weatherhead 2006). Mate switching could be the main reason of nest desertion in our populations given that most of the unfinished nests were found in the first part of the breeding season (i.e. before June).

Laying and incubation stages

In our population, females started laying at the end of May, while in southwest Germany laying begins in the second week of May (Riedinger 1974). It is likely that climatic conditions could affect this parameter since, in the Mediterranean region, Bonelli's Warblers live at higher altitudes where warmer temperatures are reached later than in the lower woodlands of central Europe (Fargallo and Johnston 1997, Sanz *et al.* 1997). We found nine days difference between mean laying date in 2013 (20 May) and 2012 (29 May). The weather conditions during the pre-laying period could affect the start of reproductive activities (Novoa *et al.* 2008) and, in fact, April in 2012 was almost 2°C colder than the 1970–2000 average, whereas it was 1°C warmer in 2013 (Spanish Meteorological Agency, AEMET). Thus, it seems likely that this is the reason for the delay of laying in 2012.

Bonelli's Warblers in Sierra Nevada had a significant smaller clutch size compared with birds from a German population (Riedinger 1974, Table 3). The increase of clutch size with increasing latitude has been documented both between and within species (Ojanen *et al.* 1978, Perrins & Birkhead 1983, Martin 1996, Cardillo 2002, Rose & Bruce 2013) and exceptions are very rare (Soler & Soler 1992). Most studies reported a negative relationship between clutch size and altitude, both at species and population levels (Badyaev 1997, Lu 2005, Lu 2008, Lu *et al.* 2009, Badyaev & Ghalambor 2001 but for exceptions see Weathers *et al.* 2002, Johnson *et al.* 2007). In general they argued that bird fecundity declines in response to the harsher environmental conditions at higher altitudes which constrained the production of eggs. However, we found the opposite pattern. We do not think that the altitude difference in clutch size was driven by laying date because this parameter did not vary with altitude. Lu (2008) found no evidence of reduction in clutch size with altitude in a related species, the Tickell's Leaf Warbler *Phylloscopus affinis*, or among other Asiatic warbler species. It could be that the same environmental pressures, such as altitude in this case, may not act in a consistent manner among or within species, and we can attribute this finding to the

differences in local condition or environmental variation, such as differences in food availability (Martin 1996) or predation pressure (Slagsvold 1982). In particular, smaller clutches at higher altitudes could be a consequence of the increase in predation along altitudinal gradients (Slagsvold 1982), although other studies showed a general decrease of predation pressure at higher altitudes (Caulson 1956, Badyaev 1997). A lower predation risk in the upper part of the study areas, possibly mediated by a higher brood replacement rate or a change in the predator community, might be responsible for the increase in clutch size of Bonelli's Warblers along the altitudinal gradient of Sierra Nevada.

Females laid fewer eggs as the breeding season advanced (Figure 2). This is a common biological trait that has also been reported in other species of the genus, both in Europe (Wood Warbler, Wesolowski & Maziarz 2009 and Chiffchaff, Rodrigues & Crick 1997) and Asia (Tickell's Leaf Warblers, Lu 2008). Smaller clutches usually occur at the end of the breeding period when conditions are less favourable and food becomes less readily availability (Garamszegi *et al.* 2004). In addition, we found a negative relationship between clutch size and egg volume, consistent with previous findings (Blackburn 1991, Soler & Soler 1992, De Neve & Soler 2002) and usually explained by the trade-off between these two parameters in terms of parental investment (Perrins & Birkhead 1983). In our population, egg volume decreased with increasing altitude but this relationship was not driven by a larger clutch size at higher altitudes given that the interaction between these predictors was not significant. Johnson *et al.* (2006) argued that smaller eggs at high altitudes could be favoured by selection to facilitate an extra energy allocation strategy, sacrificing egg size before clutch size.

Through the use of cameras, we were able to confirm information regarding important aspects of incubation behaviour. Females incubated more than 45 minutes per hour. We observed that while females incubated, males normally stayed in the proximity of the nest calling, often from regular perches. Males frequently visited the nest when incubating females were not present. Since we observed just once a male feeding a female at the nest, we can conclude that in this species males do not generally feed females during incubation. Thus, the most probable reason for interrupting incubation would be that females need to feed themselves (Ibáñez-Álamo & Soler 2012). Females living at higher altitudes spend more time incubating and this relationship was not caused by the increase of clutch size in altitude because clutch size was not

correlated with the duration of the incubation period. The colder climate at high altitudes may increase thermoregulatory needs during embryonic development and this factor could protract the duration of the incubation. Generally, high altitude birds spend more time in all parental care activities (Badyaev 1997, Badyaev & Ghalambor 2001).

The daily survival rate of nests (0.958) was similar, or slightly lower, to that found in other *Phylloscopus* species, such as Willow Warblers *P. trochilus*, Chiffchaffs or Wood Warblers (0.958, 0.978 and 0.989, respectively; Tiainen 1983, Rodrigues & Crick 1997, Mallord *et al.* 2012). Almost all eggs of completed clutches hatched (4.5 of 5 eggs), which is similar hatching success to that recorded in the Wood Warbler (5.5 of 6 eggs; Wesolowski & Maziarz 2009). The number of eggs hatched is directly related to clutch size, while a negative relationship was found between brood size and incubation period, probably because females could start incubating with the penultimate egg (pers. obs.).

Nestling stage

Fledging success, that is, the proportion of the nests in which at least one nestling fledged from successfully hatched eggs, was 0.29. The daily survival rate during nestling period (0.945) was similar to that found for Willow Warbler in Southern Finland (0.946; Tiainen 1983) but relatively lower compared with another population in Britain (0.981; Peach *et al.* 1995) or with other related species such as Chiffchaff (0.982; Rodrigues & Crick 1997) or Wood Warbler (0.969; Mallord *et al.* 2012). On average, four young fledged from every successful nest following a mean nestling period of 12.5 days; a period which is common to other warbler species (Cramp 1985). Even if both nestling and incubation periods usually increase with altitude (Badyaev & Ghalambor 2001, but see Badyaev 1997), we found this relationship only for the incubation period (see above).

We found an extremely low breeding success in our population (25%). This value is lower than that found

in two related species: 39% in a Finnish Willow Warbler population (Tiainen 1983) and 57% in a Wood Warbler population located in Wales, UK (Mallord *et al.* 2012). As the 67% of all active nests failed well before the nestlings were able to leave the nest, we are confident that most of the nest failure occurred because of nest predation. This is also supported by the fact that the majority of all unsuccessful nests found were damaged or completely destroyed, indicating the action of nest predators. Nevertheless, a more detailed study about the effect of nest predation for this species, including the identification of nest predators, will be very interesting to assist any future conservation actions.

When nestlings were about to leave the nest, they had already reached adult body mass and tarsus lengths (Table 4), but not wing length; a feature that reaches adult size after fledging (O'Connor 1984). In accordance to this, we found that nestlings that spent more time in the nest were those which grew tarsus length and gained body mass more slowly, but these patterns were not found for wing length. Furthermore, body mass and tarsus length grew more slowly at higher altitudes, while we did not find relationship for the length of the wings. This body size pattern may be attributed to constraints on individual growth due to climate severity, food scarcity and/or hypoxia at higher altitudes (Lu *et al.* 2009). Low temperatures at high altitudes impose greater energetic requirements for self-maintenance, which may limit the resources that can be allocated to growth. Low food availability could favour a decrease in nestling provisioning which could also affect growth rate and even nestling survival. According to Dillon *et al.* (2006), hypoxia may reduce metabolic activities. Since the duration of nestling period was not correlated with the altitude, nestlings raised at high altitudes fledged at the same time as those raised at lower altitudes, but they experienced slower growth rates.

Conservation aspects

Considering that the distribution of Western Bonelli's Warblers is essentially limited to western Europe, with

Table 4. Biometrics of Bonelli's Warblers *P. bonelli* in relation to age.

	Body mass (g)			Wing length (mm)			Tarsus length (mm)		
	Mean	se	N	Mean	se	N	Mean	se	N
<i>Nestlings</i>									
2–4 days	3.20	0.24	28	11.61	0.75	26	8.98	0.42	20
5–7 days	6.12	0.27	28	23.77	1.19	26	13.97	0.41	20
8–10 days	8.08	0.13	28	35.70	0.83	26	17.50	0.83	19
<i>Adults</i>	7.79	0.11	31	63.27	0.41	33	18.97	0.07	33

more than 65% of all breeding pairs in Spain, the low breeding success reported here raises an important conservation concern. It is even more relevant because the species has declined in the last few years in some parts of Europe (Dubois *et al.* 2000, Del Hoyo *et al.* 2006) and particularly in the mountain range of Sierra Nevada (Zamora & Barea-Azcón 2015). In this area, Bonelli's Warblers still represent one of the most abundant breeding passerine species (Martínez *et al.* 2010), but the population size has declined to a quarter of what it was 30 years ago (Zamora & Barea-Azcón 2015). Bonelli's Warblers live in well-defined habitats, mainly in Mediterranean mountain regions which involve many fragile and threatened ecosystems (Santos *et al.* 2002). There is no information about breeding site fidelity of Bonelli's Warblers, but three birds that were ringed in 2012 were seen in the same breed areas the following year. This suggests that Bonelli's Warblers could be relatively faithful to their breeding sites, but more data are needed. Therefore, any environmental or stochastic change could severely affect Bonelli's Warbler populations given the low breeding success found in this study, and that impact could be effective over the whole Mediterranean range. In fact, fires seem to have an important impact in the demography of this species in some regions (Urios *et al.* 1991). Both the low breeding success in this population and the threatened habitat used by Bonelli's Warblers suggest that the status of this species may easily worsen and will need close monitoring. Therefore, the novel and detailed information reported in our study about the breeding biology of Bonelli's Warblers could be crucial not only for expanding our understanding of this interesting species but also to call attention to the potential risks that it faces now, or might face in the near future (Zamora & Barea-Azcón 2015) due to a low breeding success. We suggest that we should monitor more closely its population trends and apply conservation measures if needed.

Acknowledgements

We thank Alice Squarzina and Danail Minchev Ivanov for the assistance during the field work in 2013. We thank the associate editor Richard Broughton, Catriona Morrison and one anonymous reviewer for their constructive comments.

Funding

Financial support was given by project Junta de Andalucía (research project CVI-6653). This research was conducted following relevant national guidelines (Real Decreto 1201/2005, de 10 de Octubre).

References

- Badyaev, A.V. 1997. Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oecologia* **111**: 365–374.
- Badyaev, A.V. & Ghalambor, C.K. 2001. Evolution of life history along elevational gradients: trade-off between parental care and fecundity. *Ecology* **82**: 2948–2960.
- Bell, C.P. 1996. The relationship between geographic variation in clutch size and migration pattern in the Yellow Wagtail. *Bird Study* **43**: 333–341.
- Bird Life International. 2004. *Birds in Europe: Population Estimates, Trends and Conservation Status*. Bird Life International, Cambridge.
- Bird Life International. 2014. *Phylloscopus bonelli*. The IUCN Red List of Threatened Species 2014: e.T22730987A6257507 5. <http://dx.doi.org/10.2305/IUCN.UK.2014-2.RLTS.T22730987A62575075.en>
- Blackburn, T.M. 1991. An interspecific relationship between egg size and clutch size in birds. *The Auk* **108**: 973–977.
- Bremond, J.C. 1976. Specific recognition in the song of Bonelli's Warbler (*Phylloscopus bonelli*). *Behaviour* **58**: 99–116.
- Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? *J. Anim. Ecol.* **71**: 79–87.
- Clement, P. & Christie, D.A. 2013. Western Bonelli's Warbler (*Phylloscopus bonelli*). In del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., & De Juana, E. (eds) *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. <http://www.hbw.com/node/58866> (accessed 25 July 2016)
- Costa-Tenorio, M., Morla, C. & Sainz-Ollero, H. 1998. *Los Bosques Ibéricos*. Editorial Planeta, Madrid.
- Coulson, J.C. 1956. Mortality and egg production of the Meadow Pipit with special reference to altitude. *Bird Study* **3**: 119–132.
- Cramp, S. 1955. The breeding of the Willow Warbler. *Bird Study* **2**: 121–135.
- Cramp, S. (ed.). 1985. *Birds of the Western Palearctic*, Vol. IV. Oxford University Press, Oxford.
- Cramp, S. (ed.). 1992. *Birds of the Western Palearctic*, Vol. VI. Oxford University Press, Oxford.
- De Neve, L. & Soler, J.J. 2002. Nest-building activity and laying date influence female reproductive investment in magpies: an experimental study. *Anim. Behav.* **63**: 975–980.
- Del Hoyo, D.J., Elliot, A. & Christie, D.A. 2006. *Handbook of the Birds of the World. Vol. XI. Old World Flycatchers to Old World Warblers*. Lynx Editions, Barcelona.
- Díaz, J.A., Pérez-Tris, J., Bauwens, D., Pérez-Aranda, D., Carbonell, R., Santos, T. & Tellería, J.L. 2007. Reproductive performance of a lacertid lizard at the core and the periphery of the species' range. *Biol. J. Linn. Soc.* **92**: 87–96.
- Dietzen, C., Hackenberg, C., Heyne, K.H., Sauer-Gürth, H., Staudter, H. & Wink, M. 2007. Genetically confirmed interbreeding between Western Bonelli's Warbler (*Phylloscopus bonelli*) and Wood Warbler (*P. sibilatrix*). *J. Ornithol.* **148**: 85–90.
- Dillon, M.E., Frazier, M.R. & Dudley, R. 2006. Into thin air: physiology and evolution of alpine insects. *Integr. Comp. Biol.* **46**: 49–61.
- Dubois, P.J., Le Marechal, P., Oliosio, G. & Yesou, P. 2000. *Inventaire des Oiseaux de France*. Nathan, Paris.

- Eionet. 2014. European Topic Centre on Biological Diversity. <http://bd.eionet.europa.eu/article12/summary?period=1&subject=A313>
- Fargallo, J.A. & Johnston, R.D. 1997. Breeding biology of the Blue Tit (*Parus caeruleus*) in a mountain Mediterranean deciduous forest: the interaction of latitude and altitude. *J. Ornithol.* **138**: 83–92.
- Garamszegi, L.Z., Török, J., Tóth, L. & Michl, G. 2004. Effect of timing and female quality on clutch size in the Collared Flycatcher *Ficedula albicollis*. *Bird Study* **51**: 270–277.
- Green, R.E. 2004. Breeding biology. In Sutherland, W.J., Newton, I. & Green, R.E. (eds) *Bird Ecology and Conservation. A Handbook of Techniques*, p. 57. Oxford University Press, New York.
- Helbig, A.J., Seibold, I., Martens, J. & Wink, M. 1995. Genetic differentiation and phylogenetic relationships of Bonelli's Warbler *Phylloscopus bonelli* and Green Warbler *P. nitidus*. *J. Avian Biol.* **26**: 139–153.
- Hoyt, O.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *The Auk* **96**: 73–77.
- Ibáñez-Álamo, J.D. & Soler, M. 2012. Predator-induced female behavior in the absence of male incubation feeding: an experimental study. *Behav. Ecol. Sociobiol.* **66**: 1067–1073.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *The Auk*. 651–661.
- Johnson, L.S., Ostlind, E., Brubaker, J.L. & Balenger, S.L. 2006. Changes in egg size and clutch size with elevation in a Wyoming population of Mountain Bluebirds. *Condor* **108**: 591–600.
- Johnson, L.S., Brubaker, J.L., Ostlind, E. & Balenger, S.L. 2007. Effect of altitude on male parental expenditure in Mountain Bluebirds (*Sialia currucoides*): are higher-altitude males more attentive fathers? *J. Ornithol.* **148**: 9–16.
- Li, S. & Lu, X. 2012. Breeding biology of Rock Sparrow *Petronia petronia* in the Tibetan Plateau, with special reference to life history variation across altitudes. *Acta Ornithol.* **47**: 19–25.
- Lu, X. 2005. Reproductive ecology of Blackbird (*Turdus merula maximus*) in a high altitude location, Tibet. *J. Ornithol.* **146**: 72–78.
- Lu, X. 2008. Breeding ecology of an old world high-altitude warbler, *Phylloscopus affinis*. *J. Ornithol.* **149**: 41–47.
- Lu, X., Ke, D.H., Zeng, X.H. & Yu, T.L. 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: response to more stressful environments. *J. Arid Environ.* **73**: 1103–1108.
- Maddox, J.D. & Weatherhead, P.J. 2006. Nests without eggs: abandonment or cryptic predation? *The Auk* **123**: 135–140.
- Mallord, J.W., Orsman, C.J., Cristinacce, A., Butcher, N., Stowe, T.J., & Charman, E.C. 2012. Mortality of Wood Warbler *Phylloscopus sibilatrix* nests in Welsh Oakwoods: predation rates and the identification of nest predators using miniature nest cameras. *Bird Study* **59**: 286–295.
- Martin, T.E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? *J. Avian Biol.* **27**: 263–272.
- Martínez, J.G., Iglesias, J.J., Ibáñez-Álamo, J.D., Martín-Vivaldi, M. & Soler, M. 2010. Distribución del Cuco común (*Cuculus canorus*) y sus hospedadores en Sierra Nevada (Sur de España). In *Proyectos de investigación en parques nacionales: 2006–2009*, pp. 397–408. Ministerio de Agricultura, Alimentación y Medio Ambiente, Granada.
- Novoa, C., Besnard, A., Brenot, J.F. & Ellison, L.N. 2008. Effect of weather on reproductive rate of Rock Ptarmigan *Lagopus muta* in the eastern Pyrenees. *Ibis* **150**: 270–278.
- O'Connor, R.J. 1984. *The Growth and Development of Birds*. Wiley, New York.
- Ojanen, P., Orell, M. & Väisänen, R.A. 1978. Egg and clutch sizes in four passerine species in Northern Finland. *Ornis Fennica* **55**: 60–68.
- Peach, W.J., Crick, H.Q. & Marchant, J.H. 1995. The demography of the decline in the British willow warbler population. *J. Appl. Stat.* **22**: 905–922.
- Perrins, C.M. & Birkhead, T.R. 1983. *Avian Ecology*. Blackie, Glasgow.
- Pilastro, A., Macchio, S., Massi, A., Montemaggiore, A. & Spina, F. 2008. Spring migratory routes of eight trans-Saharan passerine through the central and Western Mediterranean: result from a network of insular and coastal ringing sites. *Ibis* **140**: 591–598.
- Prince, T.D., Andreas, J., Helbig, A.J. & Richman, A.D. 1997. Evolution of breeding distribution in the old world leaf warblers (Genus *Phylloscopus*). *Evolution* **51**: 552–561.
- R Development Core Team. 2012. *R: A language and environment for statistical computing*. R foundation for statistical computing, Vienna. <http://www.r-project.org> (accessed 25 July 2016)
- Riedinger, H.J. 1974. Beobachtungen zur Brutbiologie und zum Verhalten des Berglaubsängers *Phylloscopus bonelli* auf der Schwäbischen Alb. *Anz. orn. Ges. Bayern* **13**: 171–197.
- Rivas-Martínez, F. 1987. Introduction: nociones sobre fitosociología, biogeografía y bioclimatología. In Peinado, M. & Rivas-Martínez, S. (eds) *La vegetación de España*, 18–25. Universidad de Alcalá de Henares, Madrid.
- Rodrigues, R. & Crick, H.Q.P. 1997. The breeding biology of the Chiffchaff *Phylloscopus collybita* in Britain: a comparison of an intensive study with records of the BTO Nest Record Scheme. *Bird Study* **44**: 374–383.
- Rose, P.A. & Bruce, E.L. 2013. Day length, reproductive effort, and the avian latitude clutch size gradient. *Ecology* **94**: 1327–1337.
- Santos, T., Tellería, J.L. & Carbonell, R. 2002. Bird conservation in fragmented Mediterranean forests of Spain: effects of geographical location, habitat and landscape degradation. *Biol. Conserv.* **105**: 113–125.
- Sanz, J.J. 1997. Geographic variation in breeding parameters of the Pied Flycatcher *Ficedula hypoleuca*. *Ibis* **139**: 107–114.
- Schaefer, H.C., Eshiamwata, G.W., Munyekenye, F.B. & Böhning-Gaese, K. 2004. Life-history of two African Sylvia warblers: low annual fecundity and long post-fledging care. *Ibis* **146**: 427–437.
- SEO/BirdLife. 2010. *Conservation Status of Birds in Spain in 2010*. SEO/BirdLife, Madrid.
- Skutch, A.F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithol. Monogr.* **575**–594.
- Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* **54**: 159–169.
- Soler, M. & Soler, J.J. 1992. Latitudinal trends in clutch size in single brooded hole nesting bird species: a new hypothesis. *Ardea* **80**: 293–300.

- Stutchbury, B.J. & Robertson, R.J. 1987.** Do nest building and first egg dates reflect settlement patterns of females? *The Condor* **89**: 587–593.
- Tiainen, J. 1982.** Ecological significance of morphometric variation in three sympatric *Phylloscopus* Warblers. *Ann. Zool. Fenn.* **19**: 285–295.
- Tiainen, J. 1983.** Dynamics of a local population of the Willow Warbler *Phylloscopus trochilus* in southern Finland. *Ornis Scand.* **14**: 1–15.
- Urios, V., Escobar, J.V., Pardo, R. & Gomez, J.A. 1991.** *Atlas de las Aves Nidificantes de la C.Valenciana*. Conselleria de Agricultura y Pesca, Generalitat Valenciana, Valencia.
- Valle, F. 2003.** *Mapa de Series de Vegetación de Andalucía*. Editorial Rueda, Madrid.
- Waught, D. 2002.** *Geography: An Integrated Approach*. Scotprint, Cheltenham.
- Weathers, W.W., Davidson, C.L., Olson, C.R., Morton, M.L., Nur, N. & Famula, T.R. 2002.** Altitudinal variation in parental energy expenditure by white-crowned sparrows. *J. Exp. Biol.* **205**: 2915–2924.
- Wesołowski, T. 2013.** Timing and stages of nest-building by Marsh Tit (*Poecile palustris*) in a primeval forest. *Avian Biol. Res.* **6**: 31–38.
- Wesolowski, T. & Maziarz, M. 2009.** Changes in breeding phenology and performance of Wood Warblers *Phylloscopus sibilatrix* in a primeval forest: a thirty-year perspective. *Acta Ornithol.* **44**: 69–80.
- Westneat, D.F. 1992.** Nesting synchrony by female Red-winged Blackbirds: effects on predation and breeding success. *Ecology* **73**: 2284–2294.
- Yom-Tov, Y. & Geffen, E. 2011.** Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biol. Rev.* **86**: 531–541.
- Zamora, R., & Barea-Azcón, M. 2015.** Long-term changes in mountain passerine bird communities in the Sierra Nevada (southern Spain): a 30-year case study. *Ardeola* **62**: 3–18.
- Zuur, A.F., Ieno, E.N., Waljer, N.J., Savelied, A.A. & Smith, G.M. 2009.** *Mixed Effect Models and Extensions with R*. Springer, New York.