ORIGINAL ARTICLE



Factors affecting the reproductive performance of barbary partridges in cereal croplands of Northwestern Morocco: the role of timing of breeding and vegetation cover at fine-scale

Saâd Hanane¹

Received: 5 December 2018 / Accepted: 2 June 2019 / Published online: 24 June 2019 © Institute of Zoology, Slovak Academy of Science 2019

Abstract

In Morocco, the barbary partridge (*Alectoris barbara*) is the major game species, highly valued by the nation's hunters. Until recently little was known about factors affecting reproductive parameters of this species on cereal croplands in North Africa. In 2018, 51 nests were found and analyzed across two agricultural areas of Northwestrn Morocco (AGR₁ and AGR₂). In this work, I assessed the relevance of a set of environmental and anthropogenic variables in predicting the clutch size and number of chicks hatched per nest, by means of generalised linear mixed models (GLMM). The average clutch size and hatching success per nest were 12.26 (\pm 0.57) and 9.26 (\pm 0.95), respectively. In the two sites, clutch-size increased as the date advanced, but was significantly larger in AGR₁ (13.17 \pm 0.84, *n* = 26) than in AGR₂ (11.20 \pm 0.70, *n* = 25). The number of chicks hatched per nest increased over time but also with the increase of the vegetation cover at fine-scale. Barbary partridge reproductive parameters were neither affected by landscape nor anthropogenic variables. I discuss these findings and their ecological, and future research implications. I recommended to pursuit the investigations, while considering imperatively the age/sex ratios and predation pressure.

Keywords Gamebird species · Cereal croplands · Clutch size · Hatching success · Morocco

Introduction

Effective wildlife conservation requires: (i) knowing and quantifing factors affecting reproductive parameters for proper and effective management of breeding populations, (ii) understanding population conditions, and (iii) assessing the degree of persistence of existing habitats (Newton 1979; Steenhof and Newton 2007). Information on these parameters are important when considering management of wild populations.

In North Africa, the barbary partridge (*Alectoris barbara* Bonnaterre, 1792) is a common sedentary breeding bird (Isenmann and Moali 2000; Thévenot et al. 2003; Isenmann et al. 2005) that is distributed from the Canary Islands to north-eastern Egypt (Foronda et al. 2005). The population is declining due to a combination of factors (Hanane 2018): (i) poaching (Alaoui 2001), (ii) hunting pressure (Madge and

McGowan 2002; BirdLife International 2004), (iii) habitat degradation (Alaoui 2001; Madge and McGowan 2002; BirdLife International 2004), and (iv) predation (Alaoui 2001). In Morocco, the barbary partridge is the major game species, highly valued by the nation's hunters (Hanane 2018). In North Africa, barbary partridges are closely associated with cereal crops (Maghnouj 1983, 1990; Akil 1998; Alaoui 2001) which provide nesting and feeding habitats for adults and chicks (Reitz et al. 2002; Rodriguez-Teijeiro et al. 2009; Setchfield and Peach 2016). This habitat covers 5.4 million hectares in Morocco (12% of the land area). This agricultural environment is nonetheless risky, because of several factors such as pesticide use, harvesting operations, and increased mechanization (Faria et al. 2016; Ponce et al. 2018; Stanton et al. 2018).

So far, most studies on barbary partridges focused on breeding biology (e.g. Maghnouj 1983; Alaoui 1992; Akil and Boudedja 1996; Akil 1998; Alaoui 2001; Boukrabouza 2011; Mezerdi 2011, 2015) and more recently on nest habitat selection (Hanane 2018). Little is known about factors affecting the nesting success of this game species in agricultural landscapes.

The main objective of this study was to document barbary partridge nest success in two agricultural areas in Northwestern Morocco. We investigate how clutch size and

Saâd Hanane sdhan333@gmail.com

¹ Forestry Research Center, High Commission for Water, Forests and Desertification Control, Avenue Omar Ibn El Khattab, BP 763, 10050 Rabat-Agdal, Morocco

nest success vary through the breeding season. Barbary partridge breed over a prolonged period (i.e. from March to July) and that timing of breeding may be trade-offs between climate (precipitation content), vegetation cover, and availability of food resources.

Materials and methods

Study areas

The study was conducted in two agricultural areas (hereafter "AGR1" and "AGR2") in Northwestern Morocco. These areas [AGR₁ (3000 ha) and AGR₂ (2139 ha)], 27.8 km apart from each other, are known to support important breeding populations of barbary partridges (Maghnouj 1983; Alaoui 2001). The climate is typically Mediterranean, with cool, rainy winters, and hot, dry summers (reaching, at times, 44 °C). The two sites receive 410 mm of mean annual rain, most of which falls during the winter rainy season (November-January). In these areas, the altitude ranges from 317 to 443 m a.s.l.. The landscape is mainly composed of two macrohabitats: cereal crops (80% in AGR₁ and 65% in AGR₂) and olive Olea europaea plantations (20% in AGR1 and 10.6% in AGR2). AGR2 is also composed by 10% of bare ground, 8% of vegetable crops, while the rest (6%) is occupied by a cork oak forest Quercus suber. Cereal crops are dominated by wheat (Triticum turgidum and T. aestivum), barley (Hordeum vulgare), and common oat (Avena sativa). In this agricultural mosaic, single-family houses, mostly distant from each other $(1.15 \pm 0.41 \text{ km})$, are found in the vicinity of patches of cereal crops and olive orchards. In the two studied agricultural areas, the harvesting of cereal crops is conducted in May and June.

Data collection

Monitoring took place from the beginning of March to the end of August, during the breeding season in 2018. This period was chosen because most pairs are nesting at this time (Thévenot et al. 2003; Hanane 2018). Because the species is patchily distributed across the landscape and highly secretive, the nests were located with the help of local people (gamekeepers, game managers, wheat harvesters and shepherds). This choice was based on 3 criteria: (i) availability and agreement to collaborate; (ii) homogeneous distribution and daily presence in the field; and (iii) large knowledge of barbary partridge nesting habitats. Potential nest sites were therefore identified by field collaborators based on the daily research by recording all signs of partridges' presence (e.g., droppings, frequently used passages to enter the cereal vegetation, hissing of males). Once one of the signs found, further and deeper research allows locating nests. For each nest, I georeferenced the location and elevation using a portable GPS (Magellan eXploristXL). The overall clutch size was determined by checking the nest each week (to minimize observer induced disturbance), especially when the adult was not in the nest, until the stabilisation of the number of eggs. The laving date was determined by: (i) knowing the date of the first egg laid; and (ii) back-dating from the hatching date assuming that incubation lasts 25 days (Maghnouj 1983). The hatching date was determined by two ways: (i) presence of chicks at nests; and (ii) presence of recent (1-2 days) egg breaks (half-shells in each others). The number of chicks hatched per nest was determined by counting the number of chicks at hatching, and by dividing by 2 the number of recent half-shells found at nests. Eggs were considered abandoned when they are still present at nest after the expected hatching date. When eggs disappeared before this date with the presence of Eurasian magpie (Pica pica Linnaeus, 1758) in their vicinity, they were considered as collected by this corvid. In some cases, this was comfirmed by the direct observation of this collect.

Explanatory variables

In order to determine factors affecting the reproductive parameters of barbary partridges in cereal cropland landscapes, 16 variables were selected (Table 1) to be included as explanatory factors in the models. These variables were used because they can potentially influence the nest success of barbary partridges. For landscape scale, I used a 50 m-radius as demonstrated by Hanane (2018) in a Moroccan agroforestry system, while

 Table 1
 Description of variables used in the analyses of the breeding performance of barbary partridge in agricultural areas of Northwestern Morocco

| Abbreviations | Descriptions |
|---------------|---|
| LD | Laying date |
| HD | Hatching date |
| DNT | Distance from nest to the nearest tree (m) |
| HVG | Maximum height of vegetation within 5-m plot (m) |
| VCV | % vegetation (cereals/herbaceous layer; estimated by the same investigator) |
| ELV | Elevation (m) |
| CCV | % Cereal fields (durum wheat, bread wheat and barley) |
| BCV | % Bare ground |
| OCV | % Permanent crops (olive orchards) |
| TCV | % Trees (others than fruit trees) |
| ECV | % Vegetation edge |
| UPCV | % Unpaved road (tracks) |
| DW | Distance from nest to the closest water point (natural or managed) (m) |
| DUP | Distance from nest to the closest unpaved road (m) |
| DH | Distance from nest to the closest human habitation (m) |
| DR | Distance from nest to the closest paved road (m) |
| | |

for fine-scale, I used a 5 m-radius (Hanane 2018). At this latter scale, all variables were measured in the field at the moment when the nest was first located. This choice was dictated by the fact that vegetation height can drastically change during the nesting period. Landscape scale variables were all performed using QGIS except for the elevation, which was estimated using a global positioning system (GPS) device (Garmin eTrex HC).

Statistical analyses

As a first step, I checked for possible correlations among variables by using variance inflation factors (VIFs). To prevent multi–colinearity, the variables were tested with Variance Inflation Factor (VIF) Analysis (Quinn and Keough 2002). Variables with a VIF > 5 were removed as recommanded by Zuur et al. (2009).

To examine how clutch size and number of chicks at hatching vary according to explanatory variables, I used Generalized Linear Mixed Model (GLMM) with a Poisson error distribution and log link function. Sampling plot [15 squares (1000 x 1000 m) among the 30 available were randomly chosen in AGR_1 and AGR₂] was included as a random factor in the model to avoid pseudo-replication. The number of chicks hatched was fitted to models by including the log of clutch size as an offset in the model. GLMM models were ordered by increasing Akaike information criterion corrected for small sample sizes using AICc (Burnham and Anderson 2002). I considered all models with Δ AICc lower than 2 to be equally good (Burnham and Anderson 2002). Variance explained was calculated using the methods of Nakagawa and Schielzeth (2013). I therefore calculated marginal R^2 (which describes the variance explained by fixed effects) and conditional R^2 (which describes variance explained by the full model).

One of the assumptions of parametric statistics is that observations are independent of each other [mean distance to the nearest nest was 65.07 m (\pm 5.51)]. This assumption is often violated with spatial data, so it is important to test for and, where present, subsequently address spatial autocorrelation in data prior to data analysis (e.g. Cherkaoui and Hanane 2018). Nugget to total sill ratio (NSR) was expressed as the percentage of total semivariance and was used to define spatial dependency in the data: NSR < 0.25 indicated strong spatial dependence, 0.25 < NSR < 0.75 indicated moderate spatial dependence, and NSR > 0.75 indicated weak spatial dependence (Cambardella et al. 1994). When spatial autocorrelation was encountered, we used spatial generalised linearmixed models, fitted via penalised quasilikelihood (glmmPQL). glmmPQL enables the building of spatial models with dependent data that are not normally distributed, and is among the best techniques for this kind of data (Dormann 2007). We adopted a Gaussian spatial correlation structure, but tests with exponential and spherical structures led to the same results.

All statistical analyses were performed in R-3.0.2 software (R Development Core Team 2013). I used the package 'Ime4' for fitting GLMMs (Bates et al. 2014), and package 'MuMIn' to calculate AICc (Bartoń 2015). The same package was used to calculate marginal and conditional R^2 via the function 'rsquared.glmm'. Packages 'sp', 'lattice' and 'gstat' were carried out to draw semivariograms (Pebesma 2006). The package 'MASS' was used to fit glmmPQL models (Venables and Ripley 2002). Finally, the package 'visreg' was used to plot graphs (Breheny and Burchett 2012). Means are quoted \pm standard errors.

Results

During the 2018 breeding season, 51 barbary partridge's nests were located (descriptive statistics of the measured variables are summarized in Table 2). 26 nests were located in the AGR₁ and 25 in AGR₂. In these agricultural areas, the average clutch size and number of chicks hatched per nest were 12.26 (\pm 0.57, min = 7, max = 18) and 9.26 (\pm 0.95, min = 0, max = 18), respectively. The proportion of hatched nests was 70.6% (min = 0; max =100). 15.7% of nests have been predated by the Eurasian magpie, 9.8% abandoned due to cereal harvesting and 3.9% lost for unknown reasons.

The model that best described variation in clutch-size included the laying date (mean = 62.3 ± 3.84 ; min = 10, max = 110) and site (Tables 3 and 4, Fig. 1a). The average number of eggs per nest increased gradually as the date advanced in both sites. However, and although having a same pattern of increase, the clutch size was significantly larger in AGR₁ (13.17 ± 0.84, *n* = 26, min = 7, max = 18) than in AGR₂ (mean = 11.20 ± 0.70, *n* = 25, min = 7, max = 18) (Table 4,

Table 2Descriptive statistics for variables (mean \pm SE) measured at
barbary partridge nests in agricultural areas of Northwestern Morocco

| Variable | Min. | Max. | $Mean \pm SE$ | | |
|----------|--------|---------|----------------------|--|--|
| DNT | 0.31 | 333.96 | 43.67±11.39 | | |
| HVG | 0.44 | 2.98 | 1.09 ± 0.06 | | |
| VCV | 42.00 | 98.00 | 83.66 ± 2.17 | | |
| ELV | 317.03 | 443.10 | 389.97 ± 5.11 | | |
| CCV | 15.10 | 100.00 | 73.01 ± 4.65 | | |
| BCV | 0.00 | 10.15 | 0.58 ± 0.32 | | |
| OCV | 0.25 | 83.00 | 23.21 ± 4.90 | | |
| TCV | 0.00 | 20.11 | 1.26 ± 0.65 | | |
| ECV | 0.00 | 15.35 | 1.21 ± 0.51 | | |
| UPCV | 0.00 | 10.00 | 0.73 ± 0.24 | | |
| DW | 11.45 | 786.06 | 163.45 ± 24.28 | | |
| DUP | 3.228 | 500.81 | 108.31 ± 16.29 | | |
| DH | 43.59 | 797.71 | 214.01 ± 29.13 | | |
| DR | 596.10 | 4343.26 | 1504.40 ± 142.74 | | |
| | | | | | |

| Breeding parameters | Models ^a | k | logLik | AICc | ΔAICc | wi | R ² _{GLMMm} | R ² _{GLMMc} |
|-------------------------------|---------------------|---|-----------|--------|-------|------|---------------------------------|---------------------------------|
| Clutch size | Site + LD | 4 | -98.318 | 205.00 | 0.00 | 0.94 | 0.492 | 0.566 |
| | LD | 3 | -101.132 | 211.30 | 6.39 | 0.04 | | |
| | Null model | 1 | -111.371 | 215.20 | 10.29 | 0.00 | | |
| Number of chicks hatched/nest | HD + log (VCV) | 3 | - 120.552 | 250.30 | 0.00 | 0.90 | 0.228 | 0.408 |
| | Log (HVG) | 2 | - 123.240 | 255.70 | 5.40 | 0.06 | | |
| | Null model | 1 | -138.623 | 281.60 | 31.30 | 0.00 | | |

Table 3Summary of the GLMM models describing barbary partridge breeding performance in agricultural areas of Northwestern Morocco. Forvariable acronyms, see Table 1

Fig. 1a). The semi variogram, established from the residuals of the best GLMM model, indicates a spatial pattern in the data (Table 4). When I explicitly considered spatial autocorrelation in the modeling through the glmmPQL models, the effects of laying date and site were still significant (Table 4).

In accordance with the \triangle AICc values, the most parsimonious model of hatching success included as explanatory variables the hatching date and local vegetation cover. The number of chicks hatched per nest was positively related to date (mean hatching date = 87.3 ± 4.35 ; min = 31, max = 135) (Tables 3 and 4, Fig. 1b) and local vegetion cover (Tables 3 and 4, Fig. 1c). Conversely to clutch size, I found no evidence of spatial autocorrelation in model's residuals (Table 4), which suggests that nearby nests have not the same hatching performance.

Discussion

In the present study I investigated the effects of local and landscape variables on the reproductive performance of barbary partridges in two agricultural areas in Northwestern Morocco. The results revealed that (i) clutch size was increasing over time in the two agricultural areas, but was larger at AGR₁ compared to AGR₂, and (ii) hatching performance (number of chicks per nest) was increasing over time, but also with the vegetation cover at fine-scale.

In these North African agricultural areas, we are in the presence of a gradually increase of barbary partridges clutch size over time. This pattern would be related to the presence of good breeding conditions during the months of May, June and July compared to March and April. In 2018, these two last months were relatively rainy with a total of precipitations of 156 and 128 mm, respectively. These climatic conditions would undoubtedly affect the adult conditions in the prereproductive period (Montagna and Meriggi 1991), thereby limiting the number of eggs lay per nest. In return, it is admitted that higher resources availability also lead to larger clutch sizes (Clifford and Anderson 2001; Evans et al. 2005; Spottiswoode 2009; Ong-in et al. 2016; Liu et al. 2018). This is the case of the majority of Moroccan agricultural areas where cereal harvests usually take places during May and June. This agricultural activity has however caused the abandonment of some nests (five in our case).

In addition, in summer, the weather is more settled than in March and April, thus insect availability is greater (Montagna and Meriggi 1991). These insects will serve as a feeding support for chicks at hatching (Enck 1987; Potts 2013). Generally, it seems that under good breeding conditions (less precipitations and availability of cereals) females of barbary partridge laid more eggs. Furthermore, it is also possible that breeding experience and age of partridges could play a role in this clutch size pattern. Indeed, young birds reproduce less well because they are limited by incomplete acquisition of

Table 4Estimates of the best GLMM models fitted for barbary partridge breeding performance in agricultural areas of Northwestern Morocco. See
Table 1 for variable acronyms

| Breeding parameters Clutch size | NSR | | Non-spatial model (GLMM) | | | | Spatial model (glmmPQL) | | | |
|---------------------------------------|-------|-----------|--------------------------|-------|---------|-----------|-------------------------|-------|-----------------|---------|
| | | | β -coefficient | SE | z-value | р | β -coefficient | SE | <i>t</i> -value | р |
| Clutch size | 0.432 | Intercept | 1.400 | 0.301 | 4.652 | < 0.0001 | 1.350 | 0.295 | 4.576 | 0.0002 |
| | | AGR1 | 1.400 | 0.301 | 4.652 | < 0.0001* | 1.350 | 0.295 | 4.576 | 0.0002* |
| | | AGR2 | -0.305 | 0.103 | -2.949 | 0.0032* | -0.305 | 0.097 | -3.142 | 0.0054* |
| | | LD | 0.008 | 0.002 | 3.468 | 0.0005* | 0.008 | 0.002 | 3.696 | 0.0015* |
| Number of chicks hatched/nest | 1.000 | Intercept | -8.315 | 1.841 | -4.516 | < 0.0001 | | | | |
| | | HD | 0.009 | 0.002 | 3.115 | 0.002* | | | | |
| | | Log (VCV) | 1.619 | 0.415 | 3.898 | <0.0001* | | | | |



Fig. 1 a Relationship between the clutch size and laying date in AGR1 (black line) and AGR2 (grey line). **b** Relationship between the number of chicks hatched per nest and hatching date. **c** Relationship between the number of chicks hatched per nest and vegetation cover at fine-scale

necessary skills (such as foraging), or incomplete physiological maturation (Fowler 1995). Juvenile individuals are more vulnerable than adults to various threats probably because of their inexperience (e.g. hunting, predation, Guillemain et al. 2013; Fox et al. 2015; Souchay et al. 2018). So it is likely that, in early season, those are mostly the young partridges (less experienced) that breed, while those are the old partridge (more experienced) that breed from the beginning of summer. These latters would thus wait until the presence of good conditions to invest in reproduction.

Although having a same pattern in clutch size over time, this parameter was significantly larger in AGR₁ compared to AGR₂. The difference in clutch size between these two sites would likely be related to breeding conditions which, at first glance, would be better in AGR₁ compared to AGR₂. With the presence of the Eurasian magpie in both sites, it is more possible that we assist to a more pronounced predation pressure in AGR₂ compared to AGR₁. However, I doubt this is a sufficient explanation for the pattern in clutch size I found, to the extent that there is an increase in clutch size over time. Overall, the literature mentions the negative effect of predation pressure (nest predation rate) on the clutch size (Hořák et al. 2011) as well as on population's spatial dynamics (Fuller et al. 1995; Robinson et al. 1995; Gruychev 2012). Another possible explanation is that there is a difference in the population age structure between AGR₂ and AGR₁. This latter site would be occupied by more young than would be the AGR₁ (more adults) which can affect their physiology and behaviour (Nadal et al. 2018). Further studies should clarify this and consider the young/adult ratio variable in the analysis, which may improve the value of age ratio in explaining between sites variations in partridge clutch size.

Results of our modelling approach also reveals that the hatching performance increases as the breeding season advances in the two sites. The same hatching temporal pattern was also recorded for two other patridge species, the grey partridge (Perdix perdix Linnaeus, 1758) and red-legged partridge (Alectoris rufa Linnaeus, 1758), by Potts (1980). The food availability from May (after cereal harvest) but also the improvement of the climatic conditions would undounbtedly explain this upward trend in the number of chicks hatched per nest. Several authors (Green 1984; Potts 1986; Montagna and Meriggi 1991) have announced the presence of a high chick mortality in cold and rainy springs, and when the availability of insects is reduced. This fits perfectly with our case where March and April months were very rainy. The absence of the site effect in explaining hatching performance corroborates this hypothesis. It is very likely that both the intensity of predation and food resource availability were virtually identical in the two agricultural areas, not allowing thereby to bring out an effect of site. The hatching success was positively associated with vegetation cover at fine-scale. Vegetation cover is undeniably a key factor for barbary partrige's nesting success (Maghnouj 1983), but also in other partridge species such as the red-legged Partridge (Ricci 1985; Ricci et al. 1990; Casas et al. 2009), and grey partridge (Bro et al. 2000). In Finnish agricultural landscapes, Krüger et al. (2018) have reported an increase of nest survival as days passed in another galliform's species, the common pheasants (Phasianus colchicus Linnaeus, 1758). In studying nest survival of mixed-grass prairie passerines, Davis (2005) suggests that increased

concealment due to vegetation growth may be a positive factor for certain species. The barbary partridge would a priori be one of these species that greatly benefit of vegetion cover at fine-scale. In addition, according to Ponce et al. (2018), the presence of high vegetation in the vicinity of the nest is a factor contributing to reduce nest predation. Overall, in birds, dense cover crop fields in spring may be an attractive breeding site (Wilcoxen et al. 2018).

In summary, the availability of cereals and the improvement of weather conditions would, at least partly, explain our results in both regarding the clutch size and hatching performance. However, the explication share of each of them is not known and quantified, as well as for other factors that could play a role such as the age/sex ratios and predation pressure. Research programs should be continued in order to deeply and urgently assess the role played by the population age/sex structure and predation pressure. This will be valuable in improving our understanding on the processes in which barbary partridges cope with prevailing abiotic and biotic conditions in North African cereal croplands to have good reproductive performances.

Acknowledgements I thank all collaborators for helping during the field work. I also thank two anonymous reviewers and the Editor of Biologia Journal for their comments and advice.

Compliance with ethical standards

Conflict of interest The author declares that he has no conflicts of interest.

References

- Akil M (1998) Dynamique des populations de la Perdrix Gambra (Alectoris barbara) dans la région de Yakouren (Algérie). Mémoire de Magister. Inst. Sci. Nat., Univ. Tizi-ouzou
- Akil M, Boudedja S (1996) La Perdrix gambra (Alectoris barbara) Rev. La Fôret Algérienne. Inst Nat For 1:31–36
- Alaoui MY (1992) Écologie de la ponte chez la Perdrix Gambra (Alectoris barbara) au Maroc. Gibier Faune Sauvage 9:405–415
- Alaoui MY (2001) Mise en évidence d'une race de montagne de Perdrix Gambra (*Alectoris barbara*) dans le haut-atlas marocain. Game Wildl Sci 18:451–457
- Bartoń K (2015) MuMIn: multi-model inference. R package version 1.9.13. Available at http://CRAN.Rhttp://project.org/package= MuMIn. Accessed 13 Sept 2018
- Bates D, Maechler M, Bolker B, Walker S (2014) Ime4: linear mixed-effects models using Eigen and S4. R package version 1.1–7. http:// cran.r-project.org/package=Ime4. Accessed 13 Sept 2018
- BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge
- Boukrabouza A (2011) Connaissance, conservation et gestion des populations de la Perdrix Gambra (*Alectoris barbara* Bonnaterre, 1792) au niveau de la réserve de chasse de Zéralda. Mémoire PGS. Université S.T.H.B.
- Breheny P, Burchett W (2012) Visualizing regression models using visreg. http://web.as.uky.edu/statistics/users/pbreheny/publications/ visreg.pdf. Accessed 16 Sept 2018

- Bro E, Reitz F, Clobert J (2000) Nest-site selection of Grey partridge (*Perdix perdix*) on agricultural lands in North-Central France. Game Wildl Sci 17:1–16
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information theoretic approach. Springer, New York
- Cambardella CA, Moorman TV, Novak JM, Parkin TB, Karlen DL, Turco RF, Konopka AE (1994) Field-scale variability of soil properties in Central Iowa soils. Soil Sci Soc Am J 58:1501–1511. https://doi.org/10.2136/sssaj1994.03615995005800050033x
- Casas F, Mougeot F, Viñuela J (2009) Double nesting behaviour and differences between sexes in breeding success in wild Red-legged Partridges *Alectoris rufa*. Ibis 151:743–751. https://doi.org/10.1111/ j.1474-919X.2009.00958.x
- Cherkaoui SI, Hanane S (2018) Evidence for a geographical gradient selection in the distribution of breeding Podicipedidae and Rallidae in the South-Western Mediterranean. J Nat Hist 52:2457–2472. https://doi.org/10.1080/00222933.2018.1539195
- Clifford LD, Anderson DJ (2001) Food limitation explains most clutch size variation in the Nazca booby. J Animal Ecol 70:539–545. https://doi.org/10.1046/j.1365-2656.2001.00521.x
- Davis SK (2005) Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. Condor 107: 605–616. https://doi.org/10.1650/0010-5422(2005)107[0605: NSPATI]2.0.CO;2
- Dormann CF (2007) Effects of incorporating spatial autocorrelation into the analysis of species distribution data. Glob Ecol Biogeogr 16: 129–138. https://doi.org/10.1111/j.1466-8238.2006.00279.x
- Enck JW (1987) The effect of insect abundance on gray partridge chick survivorship in New York. In: Kimmel RO, Schulz JW, Mitchell GJ (eds), Perdix IV: Gray Partridge Workshop. Minn. Dep. of Nat. Res., Madelia, pp 3–15
- Evans KL, Duncan RP, Blackburn TM, Crick HQP (2005) Investigating geographic variation in clutch size using natural experiment. Funct Ecol 19:616–624. https://doi.org/10.1111/j.1365-2435.2005.01016.
- Faria N, Morales MB, Rabaça JE (2016) Exploring nest destruction and bird mortality in mown Mediterranean dry grasslands: an increasing threat to grassland bird conservation. Eur J Wildl 62:663–671. https://doi.org/10.1007/s10344-016-1039-4
- Foronda P, Casanova J, Figueruelo E, Abreu N, Feliu C (2005) The helminth fauna of the barbary partridge *Alectoris barbara* in Tenerife, Canary Islands. J Helminthol 79:133–138. https://doi.org/ 10.1079/JOH2005277
- Fowler (1995) Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. Amer Zool 35:318–328. https://doi.org/10.1093/icb/35.4.318
- Fox AD, Kuhlmann Clausen K, Dalby L, Christensen TK, Sunde P (2015) Age-ratio bias among hunter-based surveys of Eurasian wigeon Anas penelope based on wing vs field samples. Ibis 157:391– 395. https://doi.org/10.1111/ibi.12229
- Fuller RJ, Gregory RD, Gibbons DW, Marchant JH, Wilson JD, Baillie SR, Carter N (1995) Population declines and range contractions among lowland farmland birds in Britain. Conserv Biol 9:1425– 1441. https://doi.org/10.1046/j.1523-1739.1995.09061425.x
- Green RE (1984) The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. J Appl Ecol 21:817–830. https://doi.org/10.2307/2405049
- Gruychev G (2012) Results from radio-telemetric monitoring of handreared and released Chukar partridges (*Alectoris chukar* Gray, 1830). Acta Zool Bulg 64:59–65
- Guillemain M, Fox AD, Pöysä H, Väänänen VM, Christensen TK, Triplet P, Schricke V, Korner-Nievergelt F (2013) Autumn survival inferred from wing age ratios: wigeon juvenile survival half that of adults at best? J Ornithol 154:351–358. https://doi.org/10.1007/ s10336-012-0899-y

- Hanane S (2018) Local- versus landscape-scale determinants of nest-site selection in a north African population of barbary partridge (Alectoris Barbara). Bird Study 65:495–504. https://doi.org/10. 1080/00063657.2018.1559797
- Hořák D, Sedláček O, Tószögyová A, Albrecht T, Ferenc M, Jelínek V, Storch D (2011) Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. Ostrich 82:175–183. https://doi.org/10.2989/00306525.2011.607863
- Isenmann P, Moali A (2000) Les Oiseaux d'Algérie. [Birds of Algeria.]. Société d'Étude Ornithologiques de France, Paris
- Isenmann P, Gaultier T, El Hili A, Azafzaf H, Dlensi H, Smart M (2005) Oiseaux de Tunisie. SEOF Editions, Paris
- Krüger H, Väänänen VM, Holopainen S, Nummi P (2018) The new faces of nest predation in agricultural landscapes—a wildlife camera survey with artificial nests. Eur J Wildl 64. https://doi.org/10.1007/ s10344-018-1233-7
- Liu M, Rubenstein DR, Cheong SA, Shen SF (2018) Multitasking and the evolution of optimal clutch size in fluctuating environments. Ecol Evol 8:8803–8817. https://doi.org/10.1002/ece3.4364
- Madge S, McGowan P (2002) Pheasants, partridges and grouse: including buttonquails, sandgrouse and allies. Christopher Helm, London
- Maghnouj M (1983) Contribution à l'étude de l'écologie et de la biologie de la reproduction de la Perdrix gambra (Alectoris barbara B.) dans trois régions du Maroc. Mémoire 3ème cycle, Inst. Agro. Vét. Hassan II, Rabat
- Maghnouj M (1990) Une reproduction naturelle satisfaisante de la Perdrix gambra (*Alectoris barbara*). Division de Recherches et d'Expérimentations Forestières, Rabat
- Mezerdi, F. 2011. Connaissance, conservation et gestion de la population de la Perdrix gambra (*Alectoris barbara* Bonnaterre, 1792) en Algérie. Mémoire de Magister. Université Mohamed Khider de Biskra
- Mezerdi, F. 2015. Biologie de la reproduction d'une population captive de la Perdrix gambra (*Alectoris barbara*) et dynamique des populations en milieux prés forestiers et présahariens en Algérie. Thèse de Doctorat, Université Mohamed Khider de Biskra
- Montagna D, Meriggi A (1991) Population dynamics of grey partridge (*Perdix perdix*) in northern Italy. Italian J Zool 58:151–155. https:// doi.org/10.1080/11250009109355746
- Nadal J, Ponz C, Margalida A (2018) Population age structure as an indicator for assessing the quality of breeding areas of common quail (*Coturnix coturnix*). Ecol Indic 93:1136–1142. https://doi.org/10. 1016/j.ecolind.2018.06.010
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x
- Newton I (1979) Population ecology of raptors. Buteo Books; Vermillion, SD, USA
- Ong-in T, Pierce AJ, Gale GA, Browne SJ, Savini T (2016) Nesting ecology and nest site selection of green-legged partridge. Raffles Bull Zool 64:89–97
- Pebesma EJ 2006. The gstat package. http://www.gstat.org. Accessed 13 Sept 2018
- Ponce C, Salgado I, Bravo C, Gutiérrez N, Alonso JC (2018) Effects of farming practices on nesting success of steppe birds in dry cereal farmland. Eur J Wildl 64. https://doi.org/10.1007/s10344-018-1167-0
- Potts GR (1980) The effects of modern agriculture, Nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). Adv Ecol Res 11:1–79. https://doi.org/ 10.1016/S0065-2504(08)60266-4
- Potts GR (1986) The partridge. Pesticides, predation and conservation. Collins, London

- Potts GR (2013) Some differences in the breeding ecology of Alectoris and Perdix partridges and implications for the conservation of Alectoris: a review. Avocetta 37:107–110
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- R Development Core Team 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org
- Reitz F, le Goff E, Fuzeau M (2002) Landscape selection by grey partridge (*Perdix perdix*) for nesting in the fields of French cereal agrosystems. Game Wildl Sci 19:209–220
- Ricci JC (1985) Utilization de quelques resources du milieu par les nichées de Perdrix rouge (*Alectoris rufa*) dans un agrosystème de type polycolture élevage. Gibier Faune Sauv 2:15–38
- Ricci JC, Mathon JF, Garcia A, Berger F, Esteve JP (1990) Effect of habitat structure and nest site selection on nest predation in redlegged partridges (*Alectoris rufa* L.) in French Mediterranean farmlands. Gibier Faune Sauv 7:231–253
- Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987–1990. https://doi.org/10.1126/ science.267.5206.1987
- Rodriguez-Teijeiro J, Sardà-Palomera F, Nadal J, Ferrer X, Ponz C, Puigcerver M (2009) The effects of mowing and agricultural landscape management on population movements of the common quail. J Biogeogr 36:1891–1898. https://doi.org/10.1111/j.1365-2699. 2009.02109.x
- Setchfield RP, Peach W (2016) The influence of crop tiller density on the breeding performance of a cerealnesting specialist. J Appl Ecol 53: 1430–1439. https://doi.org/10.1111/1365-2664.12704
- Souchay G, Besnard A, Perrot C, Jakob C, Ponce-Boutin F (2018) Anthropic and natural factors drive variation of survival in the redlegged partridge in southern France. Wildl Biol. https://doi.org/10. 2981/wlb.00438.10.2981/wlb.00438
- Spottiswoode CN (2009) Fine-scale life-history variation in sociable weavers in relation to colony size. J Animal Ecol 78:504–512. https://doi.org/10.1111/j.1365-2656.2008.01507.x
- Stanton RL, Morrissey CA, Clark RG (2018) Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agric Ecosyst Environ 254:244–254. https://doi.org/10. 1016/j.agee.2017.11.028
- Steenhof K, Newton I (2007) Assessing raptor nest success and productivity. In: Bird DM, Bildstein KL (eds) Raptor Management and Research Techniques. Hancock House, Blaine, pp 181–192
- Thévenot M, Vernon JDR, Bergier P (2003) The birds of Morocco: an annotated checklist. BOU Check-listno. 20. Tring: British Ornithologists' Union
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 2nd edn. Springer, New York
- Wilcoxen CA, Walk JW, Ward MP (2018) Use of cover crop fields by migratory and resident birds. Agric Ecosyst Environ 252:42–50. https://doi.org/10.1016/j.agee.2017.09.039
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.