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Anthropic and natural factors drive variation of survival in the red-legged partridge in southern France

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Understanding demographical processes underlying abundance and population size fluctuations is critical to species management. Knowing key parameters and responses to observed changes can reduce the number of realistic management scenarios. In hunted species, survival might be the targeted parameter for effective plans. The red-legged partridge *Alectoris rufa* is a native species in Mediterranean countries. The species is hunted, especially in France where some release plans are implemented. However, survival estimates are scarce there and most studies were conducted in Spain. Here, we took advantage of a radio-tracking experiment in southern France (200 birds surveyed) to estimate monthly and annual survival rates of both wild and released red-legged partridge and to investigate the temporal, spatial and individual variations in survival. We found very high annual survival rate in our island site (0.70) and low survival elsewhere (range: 0.25–0.29). We showed that age and sex were a significant source of variation in annual survival of wild birds with lower estimates for young and for females. The close survival between mainland sites with different mortality sources suggests that compensation may occur between predation and hunting mortality. However, a stronger assessment of this point is needed. Our study suggests that environment characteristics, especially landscape mosaic and predation pressure, was a driver of survival. On the island site, the red-legged partridge shows a different demographic tactics (higher survival, lower reproduction) than in mainland, suggesting an adaptation to the context (lower predation). Regarding hand-reared birds released just before the hunting season, their survival to the next spring was lower than 0.05. Such a low value raises the issue of using release before the hunting season for reinforcement purpose, especially due to negative impact through the general increase in hunting pressure it promotes. Habitat and hunting management may thus be a key to favour the red-legged partridge.

Species management relies on good knowledge of the abundance and population growth rate of targeted species. Understanding demographical processes underlying change in population growth rate is also critical to provide an accurate management plan as they inform which traits should be targeted first by managers (Mills 2012). Especially, knowing both the main driver (parameter with the highest elasticity) and the response of growth rate to observed changes in parameters will allow discrimination among a set of realistic management scenarios.

The Galliforme group is very interesting in this regard as it includes species with different life history tactics (reviewed by Trouvilliez et al. 1988) and a large number of hunted species (McGowan et al. 2012) such as the grey partridge

Perdix perdix or the willow grouse *Lagopus lagopus*. For these species, sustainable harvesting largely depends on their position along a demographic gradient with the different life history tactics (Sutherland 2001, Niel and Lebreton 2005). Sæther et al. (1996) suggested that, for precocial birds, the key demographic traits were those occurring during the breeding season. Indeed, Bro et al. (2000) and Ponce-Boutin et al. (2001) showed that both breeding female survival and reproductive success were the demographic parameters impacting the most the population growth rate in grey and red-legged partridges. Nonetheless, parameters with highest elasticity appear to be buffered against environmental stochasticity and show little variation over time (Morris and Doak 2004). One consequence is that more labile parameters can have more effect on population growth rate than parameters with higher elasticity (Koons et al. 2014). Furthermore, as these parameters can be more prone to change following management actions, they should be the focus of management actions (Nichols and Hines 2002). Applied to partridge cases where fecundity has the highest

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elasticity, programmes targeting survival may be more/as effective as ones focused on fecundity/productivity. Understanding variations in survival is thus critical to provide sustainable hunting plans for most Galliformes.

Aside temporal variation, survival may also vary over space. Structure and composition of the habitat as well as its suitability for Galliformes (food and/or cover availability, predator abundance, etc.) can be major determinants of survival (Flather and Bevers 2002). In particular, habitat features and vegetation types can provide shelters for preys in predator–prey systems, thereby limiting predation risk (Newton 1998, Kauffman et al. 2007). These features are regularly used as a management tool for hunted species. Local modification of habitat composition (e.g. modifying vegetation to provide adequate cover and invertebrate or Poaceae biomass with less shrubs and more herbaceous plants, protection of field margins) may improve prey protection and translate into an increase in adult or juvenile survival (Hagen et al. 2009, Ponce-Boutin et al. 2009).

Habitat and climatic variables thus translate into spatial and temporal variation of survival at the population scale. However, individual characteristics also induce variation in survival among individuals of the same population. Age is the most common individual factor related to survival heterogeneity with younger individuals having lower survival rates than adults (Trouvilliez et al. 1988, Souchay and Schaub 2016). Their higher vulnerability to predation and lower efficiency in foraging activities due to their inexperience likely explain the lower survival of younger birds (Newton 1998). Sex-specific survival is also noticeable in several bird species. Females usually show higher mortality than males as predicted by the parental cost hypothesis in birds (Liker and Székely 2005, Donald 2007). In Galliformes, a higher annual survival for males was found in grey partridge (Bro et al. 2000, Rymešová et al. 2012) and in hazel grouse, *Bonasa bonasia* (Montadert and Leonard 2003). At a finer scale, sex-specific differential survival follows a seasonal pattern in this grouse: females suffer high predation during the breeding season (cost of egg laying and incubation) while males suffer high predation over winter (higher vulnerability of singing males with reduced cover) (Montadert and Leonard 2003).

The red-legged partridge *Alectoris rufa* is a galliform species native from the Mediterranean area and introduced in the United Kingdom (Cramp and Simmons 1980). This is a heavily harvested species in western Europe and in particular in France with ca 1.3 M birds hunted during the season 2013/14 (Aubry et al. 2016). This huge number contrasts with the natural population size estimated at ca 600 000 individuals (Bro and Mayot 2006, Ponce-Boutin et al. 2012). To ensure hunting while maintaining natural populations, ca 3 M birds are produced in France for release purposes (Syndicat National Des Producteurs De Gibier De Chasse 2016). Given the potentially detrimental effect of releases of conspecifics on the natural population (Champagnon et al. 2012, Casas et al. 2016), hunting management plans with no or few releases are proposed in southern France to ensure both the viability of wild populations and the persistence of hunting activity (Ponce-Boutin et al. 2006). However, reliable estimates of survival rate over the full annual cycle are crucially needed to calibrate management plans and particularly

hunting management. To date, in this species, survival rates were estimated in Spain with a major focus on released individuals using a radio-tracking experiment (Alonso et al. 2005, Buenestado et al. 2009, Duarte et al. 2011, Casas et al. 2012). Furthermore, these studies were restricted to short time periods (usually the breeding season or the few months after release) due to limited battery lifespan. There is therefore a lack of knowledge about the annual survival of red-legged partridge in general and especially in France.

Here, we aimed at investigating variation in survival of wild red-legged partridges over several years to provide insights for the hunting management programmes occurring in France. More specifically, we aimed at estimating natural and hunting mortality rates of red-legged partridges according to individual states (age [first-year versus after first-year, respectively FY and AFY hereafter] and sex) and external factors (three sites with different habitat characteristics). Based on a survey encompassing the full annual cycle, we also investigated seasonal variation in survival rate. Furthermore, thanks to a release programme conducted at one of the study sites, we compared survival performances of released birds with those of wild individuals.

Methods

Study area

We radiotracked individuals in three different sites all located in southern France around the Mediterranean Sea. Game management in the studied estates was mainly dedicated to red-legged partridge hunting. Each study area illustrated a representative unit in terms of intensity of game management and/or release activity for Mediterranean France. The Porquerolles site (42°59'N, 6°12'E, 12.5 km², hereafter PO) is located on a small Mediterranean island in southeastern France. The site is managed by the Port-Cros National Park with no hunting pressure where the main terrestrial predator is the domestic cat *Felis silvestris catus*. The average breeding density of red-legged partridges in PO is 10 pairs km⁻². The Luberon site (43°52'N, 5°23'E, 30 km², hereafter LU) is limited to the Petit Luberon National Forest in southeastern France. The site is managed by the National Forestry Office with a low hunting pressure and has a large guild of predators including mammals and several protected raptor species (e.g. Bonelli's eagle *Aquila fasciata*, red kite *Milvus milvus* or hen harrier *Circus cyaneus*). The average breeding density of red-legged partridges in LU is 3 pairs km⁻². The Pailhes site (43°19'N, 3°21'E, 6 km², hereafter PA) is located in western Mediterranean France and is a predominantly agricultural landscape with high hunting pressure and control of predators (corvids, foxes and mustelids) by hunters. At this site, partridge releases and game activity are a part of the site management plan. Hunting and releases (in late August before the hunting season) occur only in PA during the study period. The hunting season for *A. rufa* starts in PA in early September and usually ends in November. Quotas are set for wild birds only and are based on counts of previous spring – released individuals are tagged to avoid confusion between wild and released birds. The average breeding density of red-legged partridges in PA is 20 pairs km⁻².

All three sites are made up of a mosaic of low vegetation height and moderate agricultural land use, alternating agricultural areas and scrubland vegetation in different proportions according to the sites. The vine-growing is the main agricultural activity on PA. Crops represent only a few plots on this site. The PO site is composed of four agricultural plains (mostly vineyards) separated by woods of Aleppo pines *Pinus halepensis*. The LU site is composed of a mosaic of very diverse environments, including dry grasslands, cliffs, deep gorges, pine, oak (*Quercus ilex*, *Q. coccifera*, *Q. pubescens*) or cedar forests, alternating with brush scrubland. A strong extensive grazing activity is practiced over large areas both to preserve biodiversity and to prevent fires.

Radio-equipped red-legged partridges

Wild red-legged partridges were caught using either decoy traps (Smith et al. 1981) or hand-net trapping at roost sites (Uppgren 1968). We equipped 197 wild red-legged partridges and 72 hand-reared partridges that were subsequently released from 2000 to 2006 (see Table 1 for a summary by site, origin, sex and age at marking). A balanced sex-ratio in radio-tracked individuals was achieved for each site and treatment (wild and hand-reared individuals), however age-ratio was highly variable between sites, ranging from 17% of FY marked in LU to 64% in PA for wild individuals. Regarding hand-reared individuals, only one among 72 equipped birds was an adult at the release date.

Birds were equipped with a necklace harness, which was size-adapted and attached with elastic bands supporting the

transmitters (HoloHil System Ltd. or Biotrack, weighting 7–11 g, ~9 months of signal). Birds were located by triangulation using a portable Yagi antenna at least twice a week during the breeding period (April to September) and once a week the rest of the year. When individuals were recovered as dead, mortality cause was classified as either due to hunting or other causes. We compiled individual detection histories on a monthly basis to estimate monthly mortality probabilities. Birds recovered dead during the 15 days following the release were excluded from the analysed dataset as this mortality might be induced by the stress of the capture and manipulation (Bro et al. 1999).

Cause-specific mortality model

We used a multi-state model based on the model of Schaub and Pradel (2004) to estimate cause-specific mortality probabilities. A major development of this model was to allow several kinds of recoveries depending on the cause of death and to estimate both cause-specific death proportion and band recoveries. However, because we radio-tracked each individual, the detection probability was equal to 1 as in the known-fate model, assuming that radio-trackers were active. Thus, we developed a multi-state known fate model taking into account transmitter signal loss.

We used five different states to describe both the status of the radio-transmitters and the status of the individual: alive with active transmitter (AA), alive with inactive transmitter (AI), newly dead due to hunting (NdH), newly dead due to other causes (NdO) and long-dead (D), i.e. birds dead for at

Table 1. Number of red-legged partridges marked by site, origin, sex and age at marking from 2000 to 2006 in southern France. FY and AFY refer to first-year and after first-year individuals.

| Site | Origin | Sex | Age | Marking year | | | | | | Total | |
|-------|----------|--------|-----|--------------|------|------|------|------|------|-------|------|
| | | | | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | | 2006 |
| Lu | wild | female | FY | | 2 | | | 3 | | | 5 |
| | | | AFY | 4 | 4 | 5 | 4 | 3 | | | 20 |
| | male | FY | 4 | 6 | 5 | 4 | 6 | | | 25 | |
| | | AFY | 3 | 5 | 5 | 1 | 4 | | | 18 | |
| | total | FY | 3 | 5 | 5 | 1 | 7 | | | 21 | |
| | | AFY | 7 | 11 | 10 | 5 | 13 | | | 46 | |
| Pa | wild | female | FY | | 9 | 5 | 4 | | | | 18 |
| | | | AFY | | 5 | | 1 | | | | 6 |
| | | male | FY | | 14 | 5 | 5 | | | | 24 |
| | | | AFY | | 12 | 4 | 2 | | | | 18 |
| | total | FY | | 10 | 1 | 3 | | | | 14 | |
| | | AFY | | 22 | 5 | 5 | | | | 32 | |
| | released | female | FY | 15 | 36 | 10 | 10 | | | | 56 |
| | | | AFY | | 11 | 10 | | | | | 36 |
| | | male | FY | 15 | 11 | 10 | | | | | 36 |
| | | | AFY | 12 | 11 | 12 | | | | | 35 |
| total | | FY | 1 | | | | | | | 1 | |
| | | AFY | 13 | 11 | 12 | | | | | 36 | |
| Po | wild | female | FY | | 6 | 2 | 2 | | | | 10 |
| | | | AFY | 3 | 12 | 9 | 1 | 2 | | 8 | 35 |
| | | male | FY | 3 | 18 | 11 | 3 | 2 | | 8 | 45 |
| | | | AFY | 4 | 5 | 4 | | | | | 13 |
| | total | FY | 4 | 9 | 12 | 2 | 4 | | 10 | 37 | |
| | | AFY | 4 | 14 | 14 | 2 | 4 | | 10 | 48 | |
| | total | FY | 7 | 32 | 25 | 5 | 6 | | 18 | 93 | |
| | | AFY | | | | | | | | | |

least one month. The AI state is an absorbing state allowing us to account for permanent emigration from the surveyed population due to loss of signal (tracker's failure, dispersion of the individual). Individuals in this state were not used afterwards to estimate mortality probabilities. As such, the absorbing state acts as a right censoring of the individual capture history. The use of the newly dead states allowed us to ensure that dead partridges could only be recovered once. Hence, using the matrix notation with rows and columns referring to states at time t and $t + 1$ respectively, the transition matrix between states is:

$$\begin{array}{c}
 AA \quad AI \quad NdH \quad NdO \quad D \\
 \begin{array}{l}
 AA \\
 AI \\
 NdH \\
 NdO \\
 D
 \end{array}
 \begin{bmatrix}
 (1-l) \times S & l & (1-l) \times m_H & (1-l) \times m_O & 0 \\
 0 & 1 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 1 \\
 0 & 0 & 0 & 0 & 1 \\
 0 & 0 & 0 & 0 & 1
 \end{bmatrix}
 \end{array}$$

Where l is the probability to lose the signal of the radio-tracker either due to loss of the tag, tracker's failure or emigration; m_H , m_O and S are respectively, the hunting mortality, i.e. the probability to be hunted, the natural mortality, i.e. the probability to die from natural causes and the survival probability, linked by the equation $S = 1 - m_H - m_O$.

All states corresponding to an active radiotracker were detectable with probability 1 while the state AI and D were not detectable. We distinguished several observations: '0' not detected, '1' detected alive, '2' detected hunted and '3' detected dead from natural causes. Thus, the associated detection matrix linking states (rows) to observations (column) was:

$$\begin{array}{c}
 0 \quad 1 \quad 2 \quad 3 \\
 \begin{array}{l}
 AA \\
 AI \\
 NdH \\
 NdO \\
 D
 \end{array}
 \begin{bmatrix}
 0 & 1 & 0 & 0 \\
 1 & 0 & 0 & 0 \\
 0 & 0 & 1 & 0 \\
 0 & 0 & 0 & 1 \\
 1 & 0 & 0 & 0
 \end{bmatrix}
 \end{array}$$

Main effect and model selection procedure

We were primarily interested in estimating cause-specific mortality rates in several populations of red-legged partridges: wild individuals from three different sites in southern France (LU, PA and PO) and captive-reared individuals released in PA. Thus, we used a site-dependent parameterization, but also origin-dependent parameters in PA to look at differences between wild and reared animals. We also included several effects for temporal variation: year; season (i.e. hunting season [three months – Sep, Oct, Nov] versus breeding season [five months – Apr, May, Jun, Jul, Aug] and versus winter season [four months – Dec, Jan, Feb, Mar]); hunt (i.e. within or outside the hunting season); breed (i.e. within or outside the breeding season).

To investigate these effects, we followed a step-down approach based on Akaike's information criterion (AIC,

Lebreton et al. 2009) from a general model. In this general model, we included a year effect, a season effect and a sex effect. For PA – where hunting and releases occurred, we added an origin effect and a hunting season effect. All effects were tested in interaction to allow different patterns in seasonal variation over the years and among sites and individuals. From our general model, we selected the level of time variation by comparing the initial model and model 21 for the year effect and models 16 and 19 for the seasonal variation in natural mortality (Supplementary material Appendix Table A1). From the best time effect, we then removed each variable of interest one by one and decided to discard the variable when the AIC of the new model decreases by at least 2 units. We first modelled loss of signal, then natural mortality, and finally hunting mortality to obtain the most supported model.

An age effect distinguishing between first-year (FY) and after first-year (AFY) is usually used in survival analysis. However, due to the data collection design (several periods of marking and monthly occasions), we had to use a complex system to code a simple age-effect with two classes. Moreover, the number of FY was relatively low so that complex models may have been over-parametrized. Thus, we decided to make a first model selection without age, to retain the most supported model and then tested for an age-effect only on this selected model.

All models were implemented using programme E-SURGE (Choquet et al. 2009). All parameters were estimated on a monthly basis and are provided with standard errors (\pm SE). Annual survival (from marking to next breeding season for FY, year-round for AFY) and associated variance were computed based on the delta method (Seber 1982).

Results

Starting from our initial model (model I, Table 2, see Supplementary material Appendix 1 Table A1 for the complete model selection), we selected a model including a hunting season effect in loss of signal, a combination of site, breeding season, age and origin effects in natural mortality and effects of age, origin and sex in hunting mortality (model 1). A close competing model (Δ AIC < 1.0) differed only by the absence of a sex effect for wild birds in hunting mortality. However, these two best models included several parameters that were not estimable due to some lack of data when the age effect was included in hunting mortality and natural mortality for LU. Thus, we chose to present hereafter results from the best full rank model (Burnham and Anderson 2002, Schaub and Pradel 2004) which was the third best model (model 3 Δ AIC = 5.5). This model differed from the model 1 by the absence of an age effect in hunting mortality and by the presence of an age effect for site PA in natural mortality. Results from models 1 and 2 are shown in Supplementary material Appendix 1 Table A2.

Monthly estimates

Monthly probability to lose the radiotracker signal was higher during autumn (0.054 ± 0.009) than during other

Table 2. Model selection of loss of signal and mortality probabilities in red-legged partridge marked from 2000 to 2006 in three sites in southern France. For each model, we give the number of estimable parameters (Np – when the model was not full rank, np is followed by an *), the deviance and associated Akaike's information criterion (AIC) and the difference in AIC (Δ AIC). Models are sorted by increasing values of Δ AIC. Only models with Δ AIC < 10 and the initial model are presented here. See ESM1, Supplementary material Appendix 1 Table A1 for the complete model selection.

| No. | Loss of signal | Hunting mortality | | | Natural mortality | | | Np | Dev | AIC | Δ AIC |
|-----|----------------|----------------------------------|------|-------------|----------------------|--------------|-----|--------|--------|------|--------------|
| | | Pailhès | Else | Luberon | Pailhès | Porquerolles | | | | | |
| 1 | hunt | H[sex × origin × age] + NH[-] | - | rep × age | origin × age | age | 17* | 1791.6 | 1825.6 | 0.0 | |
| 2 | hunt | H[R[sex × age] + W[age]] + NH[-] | - | rep × age | origin × age | age | 15* | 1796.5 | 1826.5 | 0.9 | |
| 3 | hunt | H[sex × origin] + NH[-] | - | rep | origin × age | - | 15 | 1801.1 | 1831.1 | 5.5 | |
| 4 | hunt | H[origin × age] + NH [-] | - | rep × age | origin × age | age | 15* | 1801.3 | 1831.3 | 5.7 | |
| 5 | hunt | H[origin × age] + NH [-] | - | rep | origin × age | - | 15 | 1802.5 | 1832.5 | 6.9 | |
| 6 | hunt | H[sex × origin] + NH[-] | - | rep | origin | - | 13 | 1807.6 | 1833.6 | 8.0 | |
| 7 | hunt | H[R[sex] + W[-]] + NH[-] | - | rep | origin | - | 12 | 1810.2 | 1834.2 | 8.6 | |
| 8 | seas | H[sex × origin] + NH[-] | - | rep | origin | - | 14 | 1807.0 | 1835.0 | 9.4 | |
| 9 | seas | year × hunt × sex × origin | - | year × seas | year × seas × origin | year × seas | 75 | 1736.9 | 1886.9 | 61.3 | |

Notation: seas=time effect with three seasons (hunting=Sep, Oct, Nov; other=Dec, Jan, Feb, Mar; breeding=Apr, Mai, Jun, Jul, Aug); hunt=time effect with two levels regarding the hunting season (hunting[H] versus non-hunting [NH]); rep=time effect with two seasons regarding the breeding season; age=age effect with two levels (FY=first-year, AFY=after first-year); origin=group effect for origin (released [R] versus wild [W]); sex=group effect for sex; -= constant term; x=interaction term.

seasons of the year (0.033 ± 0.004). Monthly survival was site-dependant, being higher in PO (0.975 ± 0.004) than in LU (from 0.843 ± 0.029 to 0.946 ± 0.024) and lower in PA (from 0.168 ± 0.061 to 0.954 ± 0.012). When setting hunting mortality to zero in PA, monthly survival rates are similar in LU and PA (0.945 ± 0.024 and 0.943 ± 0.013).

The monthly natural mortality rate was very low and constant over seasons in PO (0.025 ± 0.004). In LU, monthly natural mortality rate varied over seasons and was three-fold higher during the breeding season than outside (0.157 \pm 0.029 versus 0.054 ± 0.024 , Fig. 1A). In PA,

both age and origin of birds seemed to affect the natural mortality rate. First-year partridges had a higher mortality rate than older individuals (Fig. 1B). Hand-reared FY had a slightly higher natural mortality rate than wild FY (0.194 ± 0.071 versus 0.141 ± 0.058 respectively). The natural mortality rate of wild AFY was 0.046 ± 0.013 . Comparison of survival rates between wild and released adults was however impossible because no hand-reared individuals survived until adult age (and only one individual was released as adult).

Monthly hunting mortality rates were estimated to 0 in both LU and PO, consistent with the fact that hunting was not allowed at these sites. In the same way, monthly hunting mortality was null in PA outside the hunting season. During the hunting season, mortality was higher for captive-reared individuals than for wild ones (Fig. 2). Some sex-differences were found but changed in direction depending on the origin of birds: in hand-reared animals, we found that monthly hunting mortality rate was higher for males (0.832 ± 0.061) than for females (0.633 ± 0.076), whereas wild males had a lower monthly hunting mortality rate than females (0.139 ± 0.052 versus 0.335 ± 0.122). However, a large overlap of the 95% confidence intervals for wild bird estimates makes the sex effect in wild birds little supported.

Annual estimates

Based on the estimates from model 3, we computed estimates of annual survival rates (Table 3). These estimates emphasized the strong spatial variation found in monthly estimates with a high annual survival rate in PO (0.74 ± 0.02), medium-low survival in LU (0.29 ± 0.06) and low survival in PA (range: 0.17–0.36 for wild AFY). In this site, survival rates of released partridges until the next spring were very low, being < 0.03 irrespective of sex and age. For wild birds, AFY annual survival rates were higher for males than for females (0.36 ± 0.07 versus 0.17 ± 0.09 respectively), and probabilities to survive from late August to their first breeding season were 0.11 ± 0.07 and 0.23 ± 0.08 for FY females and FY males, respectively.

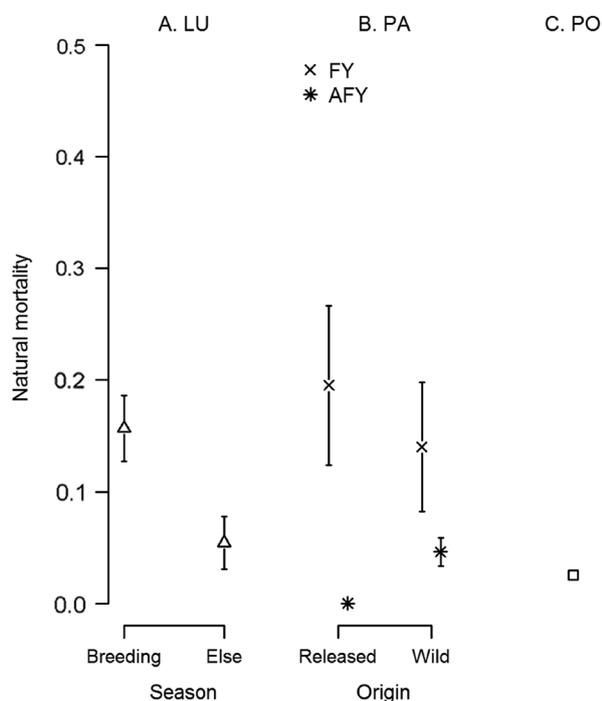


Figure 1. Monthly natural mortality rate (\pm SE) of red-legged partridges banded from 2000 to 2004 in southern France, (A) in Luberon (triangle) by season (inside or outside the breeding season), (B) in Pailhès by origin and age (cross and star for FY and AFY, respectively), (C) in Porquerolles (square).

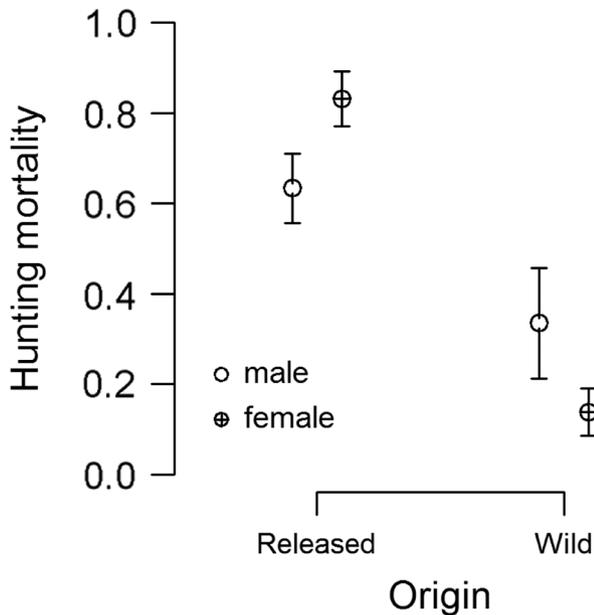


Figure 2. Monthly hunting mortality rate (\pm SE) of red-legged partridges banded from 2000 to 2003 in Pailhès, southern France, by sex and origin of birds. Triangle and squares represent female and male, respectively.

Discussion

Taking advantage of a radiotracking survey conducted over several years and at different sites, we showed the high spatial variation and within-year variation in survival of red-legged partridges. The critical period was either the hunting season or the breeding season depending on the site. Furthermore, based on the survey of released birds, we also emphasized the poor survival performance of individuals released just before the hunting season with a monthly survival being 2 to 4-times lower than that of wild birds and a survival rate until the next spring lower than 0.05.

Annual survival of wild red-legged partridge

The year-round study allowed us to obtain annual survival rates. Our values range from ca 0.25 in Pailhès to 0.74 in Porquerolles for wild red-legged partridges. These values are similar to the rates reviewed by Ponce-Boutin et al. 2001 (ca 0.30 for Pailhès and 0.71 for Porquerolles) but higher than those estimated in Spain where survival rates including hunting mortality ranged from 0.16 to 0.23 in a nine-month study (Buenestado et al. 2009). Even if they are higher than those observed in Spain, the annual survival rates we report are lower than the annual survival rates estimated in other Galliformes such as grey partridge in northern France (range: 0.40–0.60), hazel grouse (0.73) or western capercaillie *Tetrao urogallus* (0.80) (Trouvilliez et al. 1988, Bro et al. 2000). Such a low value of annual survival is consistent with a fast strategy of life history traits, which relies mostly on productivity (Sæther and Bakke 2000, Gaillard et al. 2005). However, the situation of the red-legged partridge in Porquerolles seems to be a special case. The species has a higher value of annual survival and a lower reproductive success (mean age-ratio is 0.1) than in other sites (1.6 and 2.6 in PA and LU,

Table 3. Estimates and standard error of annual survival rate of red-legged partridges by site, sex, origin and age, from model 3.

| Site | Age | Origin | Sex | Estimate (\pm SE) |
|--------------|-------------------------|-----------------------|--------|----------------------|
| Luberon | all | wild only | all | 0.29 \pm 0.06 |
| Porquerolles | all | wild only | all | 0.74 \pm 0.02 |
| Pailhès | first-year [†] | released | female | 0.02 \pm 0.01 |
| | | | male | < 0.01 \pm 0.00 |
| | after first-year | wild | female | 0.11 \pm 0.07 |
| | | | male | 0.23 \pm 0.08 |
| | | released [‡] | female | 0.03 \pm 0.02 |
| | | | male | < 0.01 \pm 0.00 |
| wild | female | 0.17 \pm 0.09 | | |
| | male | 0.36 \pm 0.07 | | |

[†]Annual survival' of first-year individuals is in fact survival from end of August to April, the beginning of the subsequent breeding season.

[‡]Due to the lack of information in our dataset to estimate natural mortality rate of released after first-year individuals, we used those of wild individuals to compute their annual survival rates.

respectively – F. Ponce unpubl.). These results are consistent with the adaptation of life history traits to an island environment (Palkovacs 2003). With reduced mortality due to a lower predation pressure, individuals are allowed to delay maturity and to grow more than in mainland before reproducing. This will in turn allow the population to increase (Palkovacs 2003). In presence of reduced mortality, adult and juvenile survival should be higher, increasing the number of offsprings. This might subsequently reduce the brood size and the number of clutch (Sæther and Bakke 2000). Our result suggest that the red-legged partridge is a very plastic species, and can adapt its life-history tactic switching from 'highly reproductive species' to 'survivor species' tactic depending on the context.

Mean annual survival rate in Pailhès (for wild AFY and irrespective of sex) was similar to annual survival in Luberon (0.25 versus 0.29) despite the fact that regulated hunting occurred in Pailhès. This suggests that compensation might occur in red-legged partridge between different sources of mortality, such as predation and hunting for instance. Sandercock et al. (2011) found evidence for partial compensation of hunting under some harvest rate threshold. Further investigations on the relationship between survival and hunting mortality are however required to test for this hypothesis.

Source of variation in survival

Beside spatial heterogeneity, we found several factors inducing variation of intra-year survival rates, including individual covariates (age, sex) and a temporal effect (season) depending on the site. The main individual effect was age: it was retained for both hunting and natural mortality in our best supported model. Despite some estimation issues in Luberon, our results suggest higher mortality for younger individuals for both sources of mortality, consistent with the hypothesis that juvenile individuals are more vulnerable than adults to various threats probably because of their inexperience (e.g. hunting, predation, Newton 2008, Guillemain et al. 2013, Fox et al. 2015).

We also detected a sex effect on hunting mortality in Pailhès, with a lower hunting mortality rate for males

than for females (Fig. 2). Similar results were found by Sandercock et al. (2011) in their study on effects of hunting in willow ptarmigan, where females had a higher risk of harvest mortality than males. Hunter selectivity has been suggested to explain this result (Sandercock et al. 2011) but is unlikely in monomorphic species such as the red-legged partridge. Several reasons can explain the sex difference in hunting mortality. First, intrinsic higher vulnerability to hunting: during the hunting season, females have lighter muscles and less power to flee away (Nadal et al. 2018) leading to potentially less efficient escape from hunters. Furthermore, breeding females might suffer more important physical depletion than males due to breeding cost, thereby decreasing their ability to escape. Second, in our study, all individuals were equipped with a radio-transmitter. Thus, the potential impact of carrying such material, added to the potential cost of reproduction, might be higher in females – the smaller sex, than in males. Third, sex-difference in habitat use during hunting seasons due to anti-predator behaviour: males could use an escape strategy while females would use a camouflage strategy in risky areas (Powolny et al. 2014). This could lead to spatial segregation by sex, similarly to territorial segregation by age observed in the red grouse *Lagopus lagopus scoticus*, (Bunnefeld et al. 2009). These hypotheses may explain the observed difference in mortality rates. However, we have no information to disentangle these reasons. Such difference in hunting mortality could lead to unintentional selective harvesting, which can have important consequences on the population dynamics (see Bunnefeld et al. 2011 for complete description in a monomorphic species). Especially, the sex-ratio before the breeding season may be skewed towards males with females having a two-fold lower annual survival rate. Fecundity could also be affected because the less abundant sex is a limiting factor for the number of breeding pairs and thus for productivity. It could also dramatically drop after some harvest threshold in the presence of selective harvesting due to a skewed sex-ratio (Bunnefeld et al. 2011) with an increase of male-male competition or breeding attempts by low quality individuals resulting in a higher number of breeding failures. In the case of the red-legged partridge in France, if a skewed sex-ratio is demonstrated, it could question the accuracy of current management plans: they are currently based on counts of singing males (Jakob et al. 2014) in spring and assume an even sex-ratio (Ponce-Boutin et al. 2006). In the presence of a significant sex-ratio bias, the number of breeding pairs might be overestimated and subsequent hunting bag limits would be too high.

We found a seasonal effect on natural mortality with higher risk of death during the breeding season than during other moments of the year but in Luberon only. Reduced survival associated with reproduction has been demonstrated in several bird species, including grey partridge, and was related to higher predation risk during the laying-nesting period (higher predation on incubating individuals and/or higher detection by predators of parents with a brood) (Bro et al. 2001, Arnold et al. 2012, Blomberg et al. 2013, Bro and Millot 2013, Wierucka et al. 2016). We thus expected to find a similar effect in the red-legged partridge. However, we found it only in Luberon, but neither in Pailhès nor in Porquerolles. The characteristics of the

latter site can explain why we found no seasonal variation in natural mortality, but the absence in Pailhès is more surprising. Natural mortality in Pailhès for AFY birds was similar to natural mortality occurring outside the breeding season in Luberon for AFY but three times lower than natural mortality during the breeding season in Luberon for AFY (Supplementary material Appendix 2 Table A2.2). Following the hypothesis that predation is the main driver of the natural mortality peak during the breeding season, lower predator densities during the breeding season (mainly due to predator control) in Pailhès than in Luberon could likely explain the absence of survival drop during the breeding season in Pailhès.

Finally, we found a significant effect of hunting in Pailhès: hunting mortality was three times higher than natural mortality (0.44 versus 0.15 for FY and 0.14 versus 0.05 for AFY) on the monthly scale, suggesting that the hunting season is a critical period of the annual cycle of red-legged partridges. Furthermore, our results indicate that young individuals are 3 times more vulnerable than adults are. However, given the close reproductive value of FY and AFY individuals in the red-legged partridge (G. Souchay unpubl.), these results suggest that hunting may have a significant impact on the population growth rate of wild populations, with a high pressure especially on young individuals.

Survival performance of released individuals

In Pailhès, we had the opportunity to monitor red-legged partridges released before the hunting season and thus to estimate and compare their mortality rate to that of FY wild individuals which are approximately of same age. The hunting mortality rate was very high (monthly estimate: 0.61–0.79) for released birds. This is 1.5–2 times higher than those of FY wild birds (see estimates for model 2 in ESM2, Supplementary material Appendix 2 Table A2.1) or than those of wild Spanish red-legged partridges (35% of the live radio-tagged juveniles at the start of the study) (Buenestado et al. 2009), and 2–3 times higher than those of Pyrenean grey partridge *Perdix perdix hispaniensis* (monthly estimate: 0.05–0.30) (Besnard et al. 2010). As for wild birds, we found a sex-effect on hunting mortality, but unlike wild birds, released males had the highest mortality rate. Such difference might arise from captivity conditions (Sokos et al. 2008, Pérez et al. 2010, 2015): captive reared birds can lose their anti-predator behaviour due to rearing in a building and/or be unable to fly properly due to lack of training. Such inability might be increased by the higher weight of captive males.

Compared to natural mortality, hunting mortality was 3- to 4-times higher (0.61–0.79 versus 0.20), following the same pattern as in wild birds. The natural mortality rate of released birds was 33% higher than that of wild birds (monthly estimate: 0.20 versus 0.15, respectively) and similar to those of released grey partridges in Switzerland in the absence of hunting (Buner and Schaub 2008). Combined, our results illustrate the higher vulnerability of released birds than wild ones to both hunting and natural causes of death, likely due to behavioural change in captive-reared individuals (e.g. loss of predator recognition, difference in escape reaction) (Sokos et al. 2008, Pérez et al. 2010, 2015).

Given that release occurred in late August, survival of released birds to the end of the hunting season (Sept–Nov) was less than 0.05. Nonetheless, subsequent seasons were more merciful with an overwinter survival rate being 0.40 ± 0.15 (from December to March). It resulted in a survival probability from release to the subsequent spring being < 0.03 , suggesting that the critical period was clearly the hunting season. We were however unable to estimate properly the AFY survival rate due to insufficient data, mainly because most of the birds died before reaching older age.

Management implications and research perspectives

Our results highlighted the important spatial variation in survival of red-legged partridge likely related to habitat. This was demonstrated in Spain where high survival was associated with high habitat heterogeneity. The survival was notably higher in more diverse areas made up of a majority of scrublands with only a small proportion of agricultural lands (Buenestado et al. 2009). Such habitats could improve survival either by creating hunting refuges or shelters against predation, one of the major causes of natural mortality and thus may be developed to favour red-legged partridge populations. Furthermore, when hunting is allowed, to create hunting reserve in high quality habitat only, may help to support wild populations of this game species.

The use of releases for hunting purposes may increase the hunting pressure on the wild populations. Previous studies (Ponce-Boutin et al. 2006, Casas et al. 2016) have shown that the number of hunting days, hunters as well as hunting bags are higher in districts where releases occur. First, the use of releases in a given district may attract new hunters due to the high probability to kill some birds, directly increasing hunting pressure (when expressed as the number of hunters/km²) in those areas. The length of hunting season may also be adjusted based on the numbers of releases. Furthermore, harvest is likely related to the number of releases individuals (Díaz-Fernández et al. 2012). However, not all released birds are shot during hunting session. Given their low survival, most of these birds will die after few days and hunters would then harvest the wild stock of red-legged partridges. Such process would likely result in an overhunting of the wild stock of birds, and in particular in the young, given their higher hunting vulnerability. Given the relative importance of young individuals for the population growth rate, a decrease of hunting pressure may favour the viability of red-legged populations. Additionally, understanding the link between hunting and survival may lead to more successful management plans for the red-legged partridge.

Our study showed that first-year survival of released birds is very low (< 0.03). At local scale, up to several hundred birds can be released (e.g. 300 in Pailhès for some years), thus on average 10 released birds may be still present at the beginning of the breeding season (for a spring population size estimated at 600 individuals). Such a situation raises the issue of potential hybridization between wild and released populations and its potential consequences on wild populations (Baratti et al. 2005, Blanco-Aguiar et al. 2008, Champagnon et al. 2013). We need to quantify both

demographic and genetic impacts of releases to ensure hunting activity and most important, the sustainability of wild populations of red-legged partridge.

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Supplementary material (available online as Appendix wlb-00438 at <www.wildlifebiology.org/appendix/wlb-00438>). Appendix 1–2.