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Original article

Hunting impact on the population dynamics of Pyrenean grey partridge *Perdix perdix hispaniensis*

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The grey partridge *Perdix perdix* used to be a common and widespread species throughout the temperate zone of western Eurasia, but its populations have markedly declined in most parts of its native range since the 1950s. The Pyrenean subspecies *P. p. hispaniensis* is threatened by alteration of its habitat, and despite ecological and hunting interest in this subspecies, the impact of harvest on population sustainability remains largely unknown. We assessed mortality of Pyrenean grey partridge and its influence on the population growth rate during 1992-2001 in the French Pyrenees. Cause-specific mortality rates were estimated using multistate capture-recapture models based on fates of 67 radio-equipped birds. Annual recruitment was estimated as the ratio of juvenile birds to adult birds in harvested samples. Mammalian predators and raptors were each responsible for a 5% monthly mortality rate. At the peak of hunting activity (i.e. October), hunting was responsible for a 30% mortality rate in some years. Modeled population growth rates appeared stable without hunting but negative with hunting. The estimated difference in population growth rates under the two regimes was 0.46. Our estimates of population growth suggest that the population was decreasing during our study, whereas it appeared stable based on ground counts. We discuss this discrepancy and proposed management actions.

Key words: cause-specific mortality, demography, grey partridge, Perdix perdix hispaniensis, population growth rate, radio-tracking, recruitment, survival

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Grey partridge *Perdix perdix* used to be a common and widespread species throughout the temperate zone of western Eurasia, but its populations have declined markedly in most parts of its native range since the 1950s (del Hoyo et al. 1994, Potts 1986). This is particularly true in the southern part of its range, where it is likely extinct in Italy and in the French Alps (Lescourret & Ellison 1987, Matteucci & Toso 1985). The Pyrenean subspecies *P. p. hispaniensis* persists with $<$ 15,000 pairs within three distinct nuclei: the Pyrenees, the northern Iberian Mountains, and the Cantabrian Mountains (Lescourret 1988, Lucio et al. 1996). In most parts of Europe their decline is due primarily to agricultural intensification (Aebischer & Potts 1994), but the Pyrenean grey partridge suffers from abandonment of agriculture in its habitat (Génard & Lescourret 1990, Lucio et al. 1996).

Pyrenean grey partridge is also a popular mountain game species in France with an annual harvest averaging 1,685 birds within the French Pyrenees (Novoa et al. 2008). To preserve the genetic integrity of this subspecies, release of hand-reared grey partridges has been restricted in the Pyrenees (Novoa et al. 2008). As a consequence, hunting is now focused on wild populations only, and it might have a negative impact on population dynamics. Despite the ecological and hunting interest in this subspecies, the impact of harvest on population sustainability in the Pyrenees remains largely unknown.

In our study, the objective was to estimate natural and hunting mortality as well as recruitment of the Pyrenean grey partridge. We used these demographic parameters to investigate the impact of hunting on population dynamics and to suggest relevant management actions.

Study area

Our study was conducted during 1992-2001 in the eastern French Pyrenees on the Soulane du Carlit (42°31'N, 1°54'E; Fig. 1), an extensive south-facing landscape where the average slope does not exceed 30%. Within this mountainous area of almost 30,000 ha, the altitude ranged from 1,300-2,800 m a.s.l. The climate of the area is continental (Izard et al. 1985) with long-term daily mean temperature of 4.8°C, and mean annual precipitation of 820 mm. Vegetation was dominated by a mosaic of shrubland (Provence broom *Cytisus purgans*, common juniper *Juniperus communis* and bearberry *Arctostaphylos uva-ursi*), grassland (red fescue *Festuca rubra*, *F. eskia* and East alpine violet fescue *F. paniculata*) and pine woodland (mountain pine *Pinus uncinata*). Cultivated areas represented $<$ 1% of our study area. The main agricultural activity was cattle grazing during June-October with pastures burned during winter to reduce shrubby encroachment. Road access within our study area was very limited. Indeed, over the 20,000 ha of study area, the use of most forestry roads is restricted and hunters may use vehicles to access areas located $>$ 2,000 m a.s.l. at only three points.

Methods

Radio-equipped partridge data

We captured, radio-equipped and monitored 76 adult grey partridges during 1992-2001. We captured birds using decoy traps in late winter and early spring (Smith et al. 1981) or spotlight and hand-nets at roost sites (Upgren 1968) in spring and autumn. We equipped partridges with necklace radio-transmitters (Holohil System Ltd.) weighing 7-11 g. We located birds from the ground at least once a week, using a portable receiver and a hand-held Yagi antenna supplemented with aerial reconnaissance when signals were lost. We classified mortalities as mammalian, avian or other unknown. Predator type was determined by examining carcasses and associated field signs, e.g. transmitters buried or not, feathers sheared off near the base, beak marks on feathers or transmitters (Caizergues & Ellison 1997).

Because trapping, handling and/or transmitters may negatively affect survival (Bro et al. 1999), we excluded censored birds dying within two weeks of tagging (Caizergues & Ellison 1997) leading to the full exclusion of nine birds which died within this time interval.

For four birds, we could not determine whether the transmitters failed or if these birds were killed by hunters without recovery of the transmitter. To avoid overestimating hunting effect, we considered these birds as transmitter failures. The analysed data set thus consists of 67 birds homogenously spread over the entire studied period (number of birds marked during 1992-2001, respectively: 6, 5, 7, 5, 11, 7, 0, 11, 8 and 3).

Grey partridge monitoring and hunting management

Each year, hunters conducted grey partridge surveys in early August with the help of pointing dogs to estimate a density index of the grey partridge population. As our study area was too large to survey entirely, birds were counted on 51 fixed survey sites, ranging in size from 0.2-0.5 km^2 and totaling 18.5 km^2. Survey sites were regularly distributed over the reproductive habitat (see Fig.1) to account for local variation in environmental conditions, and we assumed that they represented all of the available reproductive habitats (63 km^2). The density index was defined as the average number of grey partridges (adult and young) counted per 100 ha.

In the eastern Pyrenees, grey partridge hunting season runs from late September to mid-November. No shooting restrictions were in effect during 1992-1994, but during 1995-2001, shooting plans were proposed to hunters. Each year, we calculated a proposed harvest rate on the basis of results from summer counts. Harvest rates varied from one bird per 100 ha of reproductive habitat when density index was low, i.e. $<$ 15 birds/100 ha, to six birds per

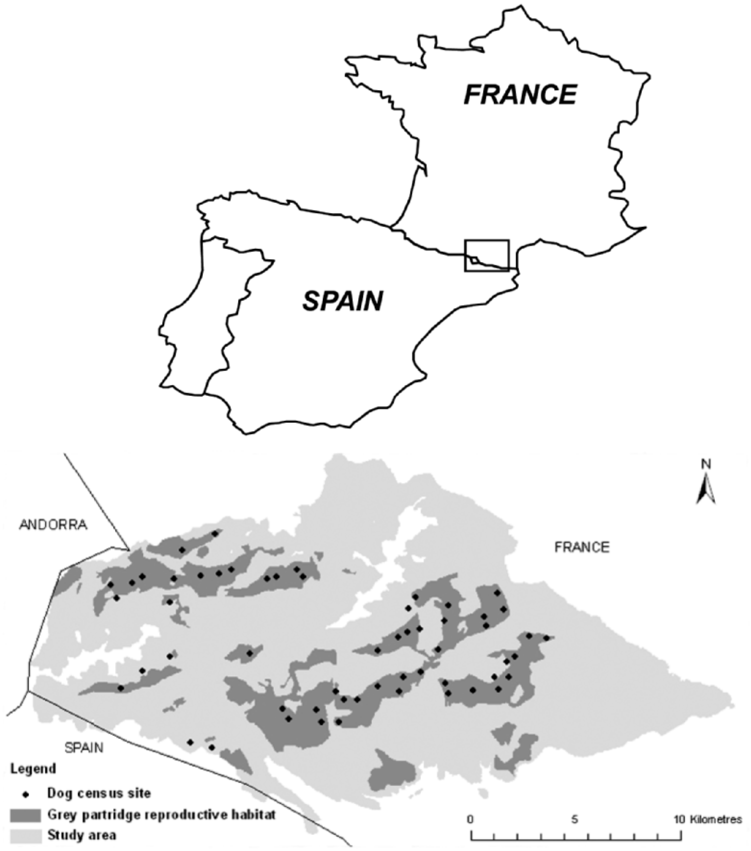

Figure 1. Study area. The figure presents the whole reproductive area of the Pyrenean grey partridge as well as the parts which are currently censused using dogs.

100 ha when density index was high, i.e. > 40 partridges/100 ha. Finally, annual shooting quotas represented between 10 and 15% of the grey partridge population in late summer.

During 1992-2001, we determined the annual age ratio of grey partridge at harvest by examination of wings obtained from hunter-killed birds. Harvested birds were classified as juveniles or adults based on the shape of their primary flight feathers (Birkan 1977). The total sample was 1,169 wings ranging from 30 in 1996 to 200 in 1993 (mean per year was 106.6 wings). Between-year differences in the number of wings collected were directly related to annual variation in hunting quotas. We did not suspect any bias in the ratio of young to adult birds within the shooting bag since hunting with pointing dogs does not select for a particular age class (Kobriger & Schulz 1992). However, we explored this hypothesis by testing whether the age ratio changes in the shooting bags over the course of the hunting season (see results).

Survival and cause-specific mortalities

We estimated cause-specific mortality using multistate capture-recapture methods used to estimate survival probabilities with competing risks of mortality (Lebreton & Pradel 2002, Schaub & Pradel 2004). In contrast to standard survival models (e.g. the Kaplan-Meier estimator or the Cox model; Elandt-Johnson & Johnson 1999), this framework provides estimates of demographic parameters that can be used in population projection matrix models (Caswell 2001).

At each observation, birds were recorded as being in one of six mutually exclusive states: alive, killed by a mammalian predator, killed by a raptor, killed by a hunter, dead due to another source of mortality (starvation or collision), or lost due to transmitter failure. A survival-transition matrix of the probabilities of moving from one state to another between observations was constructed with particular emphasis on transition probabilities from 'alive' to all the other states (Bischof et al. 2009). All states but 'alive' were absorbing states meaning that their transition probability to another state is zero.

Besides estimating transition probabilities, multistate capture-recapture models allow assessment of the influence of time and environmental factors such as weather conditions or predator abundance on mortality rates (Lebreton & Pradel 2002). We assumed monthly variation in mortality due to predation (Bro et al. 2001), but assumed constant annual mortality from predation since we do not suspect any change in predator abundance. Moreover, our data set is too small to assess such effects. We assumed that hunting-induced mortality was zero outside the hunting season, but that it varied during the hunting season. Since hunting was forbidden in a large part of our study area during 1995-1997, we also assumed reduced hunting mortality during these years and hunting mortality rates differed before and after this hunting hiatus, since shooting quotas were imposed after 1997. We considered other sources of mortality to be constant among years. Since other studies have shown that survival rates of adult grey partridge were constant after the age of three months (Birkan & Jacob 1988, Bro et al. 2000), we did not consider any effect of age on mortality.

We used different combinations of monthly and yearly effects on the mortality parameters that resulted in a set of 18 candidate models (Table 1). We used Akaike's information criterion corrected for small sample size (AIC_c; Burnham & Anderson 1998) to assess model support. We assumed models with the lowest AIC_c were the most supported models, representing the best compromise between model fit (model deviance) and its complexity (number of parameters).

We estimated survival-transition probabilities using program M-SURGE (Choquet et al. 2004). Although calculation of survival-transition probabilities explicitly accounts for imperfect detection of individuals by considering recapture probabilities, these parameters are set to 1 when using radio-marked animals.

Recruitment

The ratio of juvenile to adult birds in hunter bags provided an estimate of recruitment probability. We thus estimated recruitment during 1992-2001 using a Poisson regression of the juveniles with the number of adult birds as an offset (log-transformed) from annual counts obtained in hunter bags.

Growth rate under non-hunting and hunting regimes

We calculated the monthly survival rate in the unhunted population as the complement to 1 of the sum of natural mortalities (i.e. predation by mammals or raptors and other sources of natural mortality), and annual survival rate as the product of monthly survival probabilities. Similarly, we calculated the monthly survival rate of the hunted population as the complement to 1 of the sum of the natural mortalities for the nine months where hunting was not authorised, and the complement to 1 of the sum of mortalities including hunting during the three months when hunting was authorised. Annual survival was the product of these monthly estimates. We estimated growth rates for unhunted and hunted populations as the product of the annual survival probabilities under these two scenarios with recruitment, plus 1 for the adults of the previous year surviving over the interval.

We investigated hunting's role in a population decline, and in this case, whether a population could stabilise without hunting. In statistical terms, the answer to these two questions consisted of testing the null hypothesis that the asymptotic growth rate was equal to 1. Since our data set was relatively small, we used a parametric bootstrap procedure to generate the empirical distribution of the growth rate (Caswell 2001). Specifically, we generated 10,000 sets of random values for demographic parameters and calculated the corresponding growth rate for each set. We generated values for survival following a beta distribution which produces values between 0 and 1 and values for recruitment following a log-normal distribution which produces positive values. Parameters of these distributions were specified in such a way that their mean and standard deviation match the corresponding parameter estimate and standard error (Manly 2007). We obtained 100 (1-α)% confidence intervals for the growth rate under hunting and non-hunting regimes by finding the 100(1-α/2)th and 100(α/2)th empirical percentiles in the histogram of the simulated growth rate values (Givens & Hoeting 2005). Usually, $\alpha=0.05$ is used, and 95% confidence intervals are considered. The bootstrap procedure also allows hypothesis testing. Here, we tested the null hypothesis that growth rate was stable, i.e. was equal to 1. We rejected this hypothesis at a P-value α if the corresponding 100(1-α)% confidence interval did not contain the value 1 (Givens & Hoeting 2005).

Table 1. Model selection procedure to estimate the cause-specific mortalities of radio-equipped Pyrenean grey partridge monitored during 1992-2001 in the Pyrenees, France. Pm is the probability of predation by a mammal, Pr the probability of predation by a raptor, H the probability of being hunted. Symbol '.' means that a parameter is constant, 'm' means monthly variation on a parameter, 's' means seasonal variation, 'h' means constant except for September, October and November, 'c' means different between the 1995-1997 period when hunting was restricted and other years, and 'd' means different before 1995, between 1995-1997 and after 1997.

Model	Deviance	Number of parameters	AIC_c	Delta-AIC_c
Pm(.) Pr(.) H(h,c)	504.92	11	531.72	-
Pm(.) Pr(s) H(h,c)	499.40	14	535.48	3.76
Pm(.) Pr(.) H(h,d)	501.89	14	537.97	6.25
Pm(.) Pr(s) H(h,d)	494.16	17	540.65	8.93
Pm(s) Pr(.) H(h,c)	505.49	14	541.57	9.85
Pm(s) Pr(s) H(h,c)	497.60	17	544.09	12.37
Pm(s) Pr(.) H(h,d)	500.25	17	546.74	15.02
Pm(.) Pr(m) H(h,c)	483.32	22	550.32	18.60
Pm(s) Pr(s) H(h,d)	492.36	20	550.62	18.90
Pm(.) Pr(m) H(h,d)	478.08	25	559.79	28.07
Pm(m) Pr(.) H(h,c)	495.66	22	562.66	30.94
Pm(s) Pr(m) H(h,c)	481.51	25	563.22	31.50
Pm(m) Pr(s) H(h,c)	487.77	25	569.48	37.76
Pm(m) Pr(.) H(h,d)	490.42	25	572.13	40.41
Pm(s) Pr(m) H(h,d)	476.28	28	575.02	43.30
Pm(m) Pr(s) H(h,d)	482.53	28	581.27	49.55
Pm(m) Pr(m) H(h,c)	471.75	32	597.87	66.15
Pm(m) Pr(m) H(h,d)	466.51	35	617.80	86.08

Results

The age-ratio in the shooting bags did not change over the hunting period (time effect $P=0.29$), and we can thus conclude that there is no age-selection by hunting.

Of the 67 radio-marked partridges, 35 were killed by predators (18 were killed by mammalian predators and 17 by raptors). Predation occurred regularly throughout the year (seven mortalities between January and March, nine between April and June, nine between July and September, and ten between October and December). Eleven birds were shot by hunters.

The model selection procedure showed that the natural causes of mortality were constant over the year, whereas the hunting impact changed within and among years (see Table 1). Parameter estimates using the best model showed that monthly mortality caused by mammalian predators and raptors was about 5% for each cause. The effect of hunting was greatest in October when it was responsible for a 30% mortality rate (Table 2). Annual recruitment estimates revealed a mean of 3.20 juveniles per adult ($SE=0.47$, ranging from 1.5 to 4.9).

Median population growth rate without harvest was estimated at 1.11 ($SE = 0.25$), and the population was stable ($P = 0.35$, two-sided test). Conversely, median population growth rate with hunting was estimated at 0.65 ($SE=0.19$), and a test for a population decrease with hunting was significant ($P = 0.024$, one-sided test). Thus, hunting appears responsible for a 0.46 ($SE = 0.15$) mean decrease in population growth rate (Fig. 2).

The summer counts show that the population

Table 2. Estimates of the cause-specific mortalities of radio-equipped Pyrenean grey partridge monitored during 1992-2001 in the Pyrenees, France based on the most supported mortality model. This model included constant mortality from mammals and raptors while hunting mortality varied among months of the hunting season, and was constant during the non-hunting season, and differed between years with restricted hunting (closed years) and other (normal) years.

Parameter (monthly mortality)	Estimate	SE
Depredated by mammals	0.051	0.012
Depredated by raptors	0.048	0.011
Other sources of death	0.008	0.005
Hunting in September - normal years	0.053	0.051
Hunting in October - normal years	0.296	0.088
Hunting in November - normal years	0.059	0.057
Hunting in September - closed years	0.000	-
Hunting in October - closed years	0.000	-
Hunting in November - closed years	0.067	0.064
Transmitter failure	0.051	0.012

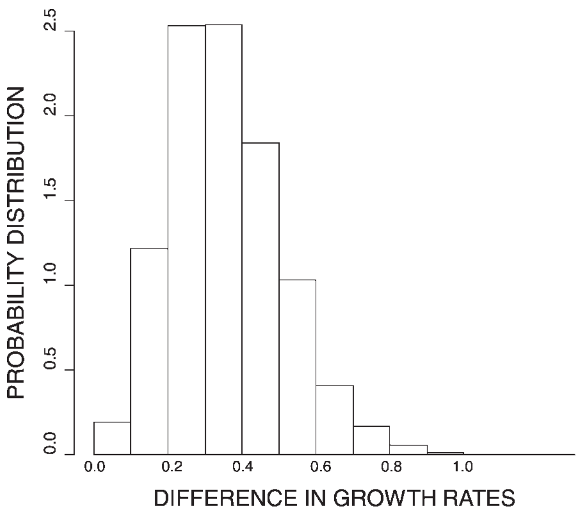

Figure 2. Difference between the growth rates of a Pyrenean grey partridge under unhunted and hunted regimes based on the demographic parameters estimated during 1992-2001 in the Pyrenees, France. The columns represent from left to right 1992-2001.

sharply decreased between 1993 and 1995. From 1995 to 1997, hunting was strictly prohibited, and after 1997, shooting quotas have been imposed. This procedure results in a rapid increase during 1995-1998, even if some large fluctuations have been observed, and to a relative stability since then (Fig. 3).

Discussion

When managing hunted species, it is especially important to evaluate the impact of harvest on population dynamics (Aebischer 1997) in order to be sure that the harvesting is sustainable. This evaluation can be conducted by estimating the different sources of mortality and considering the growth rate of the population under harvested and unharvested scenarios (Williams et al. 2002). Bro et al. (1999) showed that the negative effect of radio-transmitters on survival of grey partridge varied between years. They suggested estimating mortality rates using all radio-equipped animals and estimating rates excluding some data collected a few days following capture. The first option represents the upper limit of natural mortality whereas the latter overestimates natural survival. As we were mainly interested in estimating population stability and the effect of hunting, we excluded all data obtained during the first two weeks after capture (Caizergues & Ellison 1997). This procedure is conservative in studying the growth rate of a hunted population since natural mortality is larger or at least equal to our estimate, and therefore, it probably represents the upper limit of population growth rate.

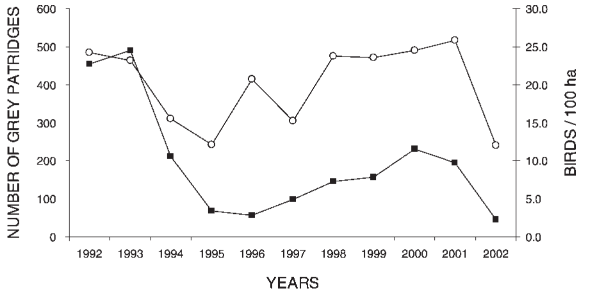

Figure 3. Summary of summer counts (○) and hunter shooting bags (■) collected on Pyrenean grey partridge during 1992-2001.

Among the 67 radio-equipped partridges in our study, only one died from starvation and two from collision with fences. Predation was the main cause of mortality (71%), compared to hunting (22%). Our results agreed with several studies which demonstrated that predation, especially by raptors can be high in game birds (Bowker et al. 2007, Valkama et al. 2005). Our estimates also fell between the 30-40% (Bro et al. 2001) and 70% (Reitz et al. 1992, Smith & Willebrand 1999) raptor mortality rates reported in other studies. With a mortality rate of 30% in only one month (October) induced by hunting compared to a 10% mortality rate a month induced by predation, our results also agree with those of Watson et al. (2007) who estimated that hunting was a much higher risk than predation in a study area in England during winter. Although seasonal variation in mammalian and raptor predation rates occurs in several game species (Bro et al. 2001, Watson et al. 2007), we did not detect monthly or seasonal differences in mortality rates caused by predation. This is likely due to a lack of statistical power associated with our small sample size.

The use of radio-transmitters allowed us to recover three birds that were shot, but not recovered by hunters. Our estimate of hunting mortality is thus not restricted to individuals recovered and includes crippling losses. The sample size (three out of 11) is too small to provide a reliable estimate of crippling loss, but this result suggests that hunter harvest is underestimated when only hunted bag censuses are used. This result is close to the 26% of crippling losses estimated for black grouse *Tetrao* *tetrix* in France (Watson 2007). Shooting quotas should thus be estimated by taking potential wounding loss into account (Birkan & Jacob 1988).

Although confidence intervals for growth rates with and without hunting were quite large, they suggested that the non-hunted population was stable whereas it declined for the hunted population. The difference between growth rates under the two regimes was large (mean 0.46) and suggested an important effect of hunting on population dynamics. Moreover, we assigned several ambiguous losses of radio-tracked birds to the state 'radio-transmitter failure' although some of them could have been due to hunting. We thus may have underestimated hunting mortality. Our estimate of a 30% hunting mortality rate in October means that a third of the population is harvested during that month.

The fact that hunting restrictions applied during 1995-2001 resulted in an immediate and positive effect on population trend suggests that growth rate in absence of hunting is $>$ 1 and this re-enforces the validity of our finding of a substantial impact of hunting on the partridge population. Nevertheless, hunting pressure has been regulated by shooting quotas since 1995, and annual summer counts suggest that despite high fluctuations, the population remains relatively stable (see Fig. 3; Novoa et al. 2008). As observed from age ratios in shooting bags, recruitment is highly variable and should be responsible for the large fluctuations in summer population size whereas shooting quotas should stabilise the population.

Our very low growth rate estimate for the hunted population contrasts to the apparent stability since 1996. Several reasons could explain this discrepancy. First, as a consequence of regulated shooting quotas, the number of harvested birds has decreased sharply (e.g. 455 birds were harvested in 1992 and only 56 in 1996; see Fig. 3). We did not detect a difference between mortality rates caused by hunting before 1995 (without quota) and after 1997 (with quota), but this is likely due to a lack of statistical power due to limited data. Our estimate of population growth rate for the hunted population is an average over the entire period, with differential quotas over the years. Growth rate estimates may be slightly overestimated for the 1992-1994 period when a sharp decrease occurs and underestimated for the 1997-2001 period. Secondly, density-dependence could limit the effect of hunting on the population. Density-dependence is an important demographic phenomenon for recruitment (Rands 1987), brood production rate (Panek 1997, Potts 1986), nest losses (Aebischer 1991) and overwinter survival rate (Aebischer 1991, Rotella et al. 1996, Tapper et al. 1996). However, Bro et al. (2000) did not detect density-dependence effects on grey partridge survival probabilities. Moreover, the detection of density-dependence effects on survival raises some statistical concerns such as underestimating its strength due to errors in the measurement of population size or even worse, missing its effect by using a too simplistic parametric shape for modelling the relationship between survival and density (Barker et al. 2002). We thus did not test for effects of density-dependence on survival, but we suspect that this mechanism could explain the unexpected patterns we observed. Bro et al. (2003) as well as Aebischer (1997) detected some density-dependence effects on several reproductive parameters. We could not explore potential density-dependent effects on recruitment because of the absence of reliable estimates of density in our study. Eventually, the Pyrenean grey partridge population decrease due to a low local population growth rate could be compensated for by density-dependent immigration of individuals born outside our study area (Smith & Willebrand 1999). Our study area was 20,000 ha and probably included most of the population and thus we do not suspect substantial levels of immigration. However, immigration could also occur at a local scale. Indeed, the 20,000 ha of our study area were not equally accessible either for logistical reasons (road access) or because of hunting refuges that eliminated hunting in $>$ 25% of our study area. Because of practical constraints related to radio-monitoring, our field efforts were mainly concentrated in relatively accessible areas. Being accessible, these zones are probably also those where hunting pressure is the heaviest. We therefore suspect that less harvested subpopulations may provide potential migrants to compensate for hunting losses.

Management implications

Up to 30% of the population of grey partridge seemed to be harvested in one month in our study site. Such a harvest rate was probably incompatible with the long-term persistence of the population. Indeed, the large population decline in the first part of our study suggests that harvest was too high for maintenance of the population. Reduction of hunting mortality after 1994 allowed the population to rapidly return to a level comparable to that observed at the beginning of our study. Since 1995, shooting quotas have been imposed and the population level appears stable, despite relatively large fluctuations in population size (see Fig. 3 and Novoa et al. 2008). Nevertheless, population size is highly dependent on breeding success, and could decrease rapidly if a low reproduction occurred. We recommend that a management strategy targeting a harvest of < 15% of August partridge densities should be maintained to maintain relative stability. We also recommend that some areas, > 100 ha and located in good reproductive habitat, be closed to hunting to maintain a source population as a precaution against possible excessive future harvest.

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