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Evidence for an additive effect of hunting mortality in an alpine black grouse *Lyrurus tetrix* population

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In the Canton of Ticino in southern Switzerland data from the monitoring programme for black grouse from 1981 to 2016 (population density, lek size, sex ratio in chicks and adults) were analysed together with information on bag statistics and hunting regulations to evaluate if mortality from hunting had an additive effect. In the study population the proportion of cocks at the beginning of the study period was only 23%. As hunting regulations for black grouse were tightened in the late 1970s the observed proportion of males showed an increase in particular during the first years but remained much lower than what would be expected from the sex ratio among chicks assuming equal survival between the sexes. The observed low proportion of adult males indicates a lower survival rate and as a consequence a smaller than natural lek size. High reproductive success two years before had a positive effect on lek size. The correlation coefficient between hunting bag and population size index increased with increasing hunting pressure and showed a decline over the years. Bag size in the period with a high hunting pressure (1981–1999, many hunting days) was driven by population density whereas in the second period (2000–2016, few hunting days) it was driven by hunting regulations. Our analysis showed that hunting affects population structure and presents indirect evidence that mortality due to hunting is additive. The study also shows that hunting management has to be continuously adapted to changes in the size and structure of the population as well as changes in habitat conditions. It is therefore essential to continue long-term monitoring of population size and of demographic parameters.

It is generally accepted that harvesting of animal populations through hunting has to be sustainable in the long term although there is still much debate over the concept of sustainable exploitation of populations (Sutherland 2001) and better communication on experience with management measures would be desirable (Moss et al. 2010). In the discussion about sustainable harvesting the following two principles are considered important:

1. Compensatory versus additive hunting-induced mortality. The concept of 'compensatory mortality' implies that the loss of individuals through hunting is compensated by an increase in average survival probability of the remaining individuals and/or by an increase in reproductive success (Sutherland 2001). The concept requires that reproduction and survival are regulated by density-dependent processes (e.g. predation, starving) and that the loss does not exceed the demographic ability of a population to compensate for the losses. If mortality is compensated by an increase in survival of the remaining individuals, mortality from hunting and from other factors are negatively correlated (Williams 1997, Péron 2013). For grouse there is hardly any evidence for a compensation of mortality via increase in reproductive output (Ellison 1991). Reviews of studies on a large variety of species indicate that pure compensation hardly exists and mortality caused by exploitation is almost always both compensatory and additive (Sutherland 2001, Péron 2013).
2. Increasing populations can be exploited sustainably if harvest rate is not higher than the long-term growth rate (Wade 1998). Population size can thus remain stable but below the ecological carrying capacity (Caughley and Sinclair 1994). As a consequence a population may become more vulnerable to stochastic events (e.g. extreme weather events), which is particularly problematic in small populations and threatened species.

The management of harvested wildlife populations aims at protecting populations from overexploitation while at the same time allowing a sustainable harvest in the long term. The most frequently used management measures aim at regulating hunting pressure through limiting bag size or hunting season length or a combination of both (Newton 1998). Monitoring of harvest but more importantly of the populations is essential to prevent populations from being overexploited (Sutherland 2001).

Careful management is particularly important where hunting is not an essential activity for providing food for a human population but is carried out purely as a hobby. The latter is the case for hunting of birds in Switzerland. From an ecological point of view hunting of stable or increasing bird populations is acceptable if it takes into account the conservation status of the species at European and national levels and if it does not negatively affect the distribution, population size and social structure of the populations (Robin et al. 2017).

Hunting of black grouse populations in Switzerland has a long tradition. Since the introduction of the Federal Act on Hunting and Conservation in 1926 black grouse hens are protected. Spring hunting of cocks was banned in 1962. Since then the hunting season at national level has been restricted to the period 1 September to 15 December, since 1988 to the period 16 October to 30 November. Cantons can fix tighter restrictions within the framework of the federal legislation. Hunting of black grouse has been banned in more and more cantons but remains legal in four cantons in the core area of its distribution in the Alps, with only the three cantons of Grisons, Ticino and Valais showing substantial bag sizes. Black grouse is classified as Near Threatened NT on the national Red List (Keller et al. 2010b) and as a species of national conservation concern requiring targeted conservation action (Keller et al. 2010a). Particular attention has therefore to be given to possible effects of hunting on the populations.

In the Canton of Ticino in southern Switzerland black grouse are mostly hunted with pointing dogs. Hunting regulations were tightened following a strong decline of harvested individuals in the 1970s to reduce a suspected negative impact of hunting on the population. In several steps the number of hunting days was reduced from 23 in the 1980s to nine at the beginning of the 21st century. The first bag limits, i.e. the maximum number of cocks per hunter and year were introduced in 1964 with eight cocks, then further reduced to six in 1971, four in 1977, and three in 1991. In parallel to the restrictions the number of hunting licences decreased as well (Zbinden and Salvioni 1997). Since 1981 the cantonal wildlife office has not only been collecting information on hunting bags but also on population size and demographic parameters, which allowed us to use the data from 1981 onwards to study the effects of hunting on population size and structure.

Studies on different galliform species have tested whether mortality due to hunting should be judged as compensatory or as additive but results and interpretations were often controversial. This is partly due to the fact that in studies without marked individuals causes of mortality other than that due to hunting are usually not known.

Studies on effects of hunting on population structure of grouse, however, are rare (Ellison and Magnani 1985). Changes in population structure may affect populations in the long term and thus be an indicator that hunting is not sustainable. If, for instance, the genetically fittest individuals are killed, this could affect reproductive output and thus population growth rate. Here we study two possible effects of hunting on population structure, namely on sex ratio and lek size.

In natural, not hunted populations, black grouse have a balanced sex ratio of 1:1 (Ellison and Magnani 1985, Marti et al. 2016). Since in our study population only cocks are hunted, an unbalanced sex ratio, i.e. a lower proportion of males in the population would indicate an additive effect of hunting mortality. Here, we compare the observed temporal development of the adult sex ratio with a theoretically expected development if males and females had equal survival based on the observed sex ratio in juveniles in autumn before the hunting season.

Further, because black grouse cocks display on leks where females choose partners for copulating (Hjorth 1970, Kervinen et al. 2016), lek size is important for the population dynamics. Large leks allow hens a choice for the fittest males. In contrast to spring hunting, which has a direct effect on local lek size, hunting in autumn could affect lek size in the following spring due to effects on the density of males. We therefore tested whether the density of cocks influences lek size in order to describe a potential pathway of the effect of hunting on population dynamics.

In this paper we combine the different analyses on effects of hunting on population density, sex ratio and lek size to evaluate whether mortality from hunting had an additive effect on black grouse populations in the Ticino and whether these effects changed over the study period of 36 years as a consequence of changes in hunting pressure..

Methods

Data recorded in the field

The analysis is based on data from the black grouse monitoring project run by the 'Ufficio della caccia e della pesca del Cantone Ticino', the cantonal wildlife office, in southern Switzerland. The same office also provided bag statistics and information on hunting regulations. The overall study area, the Canton of Ticino, covers an area of 2812 km^2 and stretches from the main ridge of the Alps south to the foothills at the border to Italy, where the black grouse reaches the edge of its range. Bag statistics were available for the whole study area. Analyses related to counts and population structure were carried out separately for the regions of 'Northern Ticino' and 'Central/Southern Ticino'. The border between these two regions corresponds to the limit between the biogeographic regions 'Southern Alps' and 'Southern Ticino' determined on the basis of faunistic and floristic criteria (Gonseth et al. 2001).

Data were available from the start of the project in 1981 up to 2016. Counts of displaying cocks in spring were carried out annually in nine census areas with a total surface of ca 50 km^2, distributed across the whole canton, with five areas in Northern and four in Central/Southern Ticino (Fig. 1). Cocks and the size of the leks were recorded from fixed observation points in the second half of May (for details see Zbinden and Salvioni 2003). The observation points were selected so that the whole census area could be surveyed simultaneously by the different observers without having to move between points. In 28 cases (out of a total of 324 censuses) counts could not be carried out due to high avalanche risk or adverse weather conditions.

Reproductive success was determined in the second half of August/early September in collaboration with hunters owning

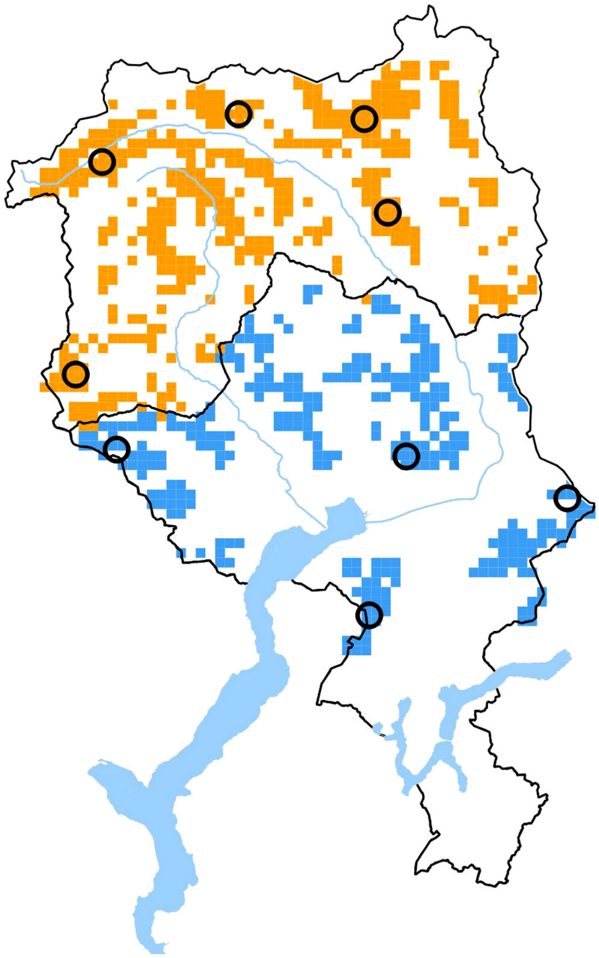

Figure 1. Map of the Canton Ticino showing the spring census areas (black circles) and the km² in which surveys with dogs were carried out in late summer (orange: Northern Ticino, blue: Central/Southern Ticino).

well-trained pointing dogs (mostly English setter or pointer). Dogs search for grouse and indicate to the hunter the location of the birds, which can then be flushed. In mid-August almost all chicks are able to fly, which allows reliable counts of the number of chicks per hen and often the determination of their sex. In addition to families, hens without chicks and cocks were also recorded. Hunters got a special licence for this activity and were attributed areas with known occurrence of black grouse. In total, data from 414 km² in Northern Ticino and 300 km² in Central/Southern Ticino, the majority of which were open for hunting, were available to analyse adult sex ratio (Fig. 1).

Statistical analyses

Population trends

Population trends were calculated with a Poisson regression using the programme TRIM, which also allows to interpolate missing values (Pannekoek and van Strien 2001). Population indices reflect only population size of cocks, because it was not possible to record females quantitatively.

Quantification of hunting pressure

We combined the four variables that reflect aspects of hunting pressure to get an index of hunting pressure using a principal component analysis for the parameters 1) starting date of the hunting season ('starting date'), 2) allowed cocks per hunter ('allowed cocks', 3) number of hunting days ('hunting days'), and 4) number of hunting licenses ('licenses'). The principal components were based on the correlation matrix because the four variables had different units. The first principal component explained 88% of the total variance among the four measurements for hunting pressure (Table 1). The second principal component explained only 9% of the variance. All four variables had approximately equal weight in the first principal component (around 0.5). Starting date had the opposite effect on hunting pressure compared to the other variables. We used the negative value of the first principal component as an index of hunting pressure for the following analyses. The principal component was multiplied by –1 for better interpretability (high values meaning high hunting pressure).

Sex ratio of black grouse chicks

For Northern Ticino data were available for 716 families, for Central/Southern Ticino for 510 families. We assumed a binomial distribution for the number of males among black grouse chicks and used a uniform prior distribution for the proportion of males to obtain its posterior distribution using the Bayes theorem. The 2.5% and 97.5% quantiles of the posterior distribution are given as lower and upper limits of the 95% credible interval.

Sex ratio of adult black grouse in relation to hunting pressure

The proportion of males among the adults was analysed by a generalized linear model. The number of males was assumed to be binomially distributed. We used the logit link function to relate the proportion of males linearly to hunting pressure (first principal component), year and region. Before the analysis, we z-transformed the variable year (subtraction of the mean and subsequent division by the standard deviation). We included year as predictor in the model to account for any potential systematic trend in sex ratio that is not related to changes in hunting pressure. Model assumptions were assessed by standard residual plots. Additionally we compared the residual degrees of freedom with the residual deviance to check whether the variance in the data corresponded to the binomial variance assumed by the model.

Change in sex ratio with and without hunting

To compare the development of the sex ratio with a theoretically expected sex ratio, we modelled the changes in sex ratio over time assuming equal survival rate of males and females. We further assumed that the survival probability of juveniles was half of that of adults (Caizergues

Table 1. Loadings of the variables for the four principal components. Loadings with values lower than 0.1 are not given.

	Comp.1	Comp.2	Comp.3	Comp.4
Starting date	0.453	0.889		
Allowed cocks	–0.509	0.305	0.772	–0.227
Hunting days	–0.517	0.198	–0.591	–0.586
Licenses	–0.518	0.279	–0.224	0.777
Proportion of variance explained	0.875	0.090	0.024	0.012

and Ellison 1997, Baines 2007, Bowker et al. 2007) and that the proportion of males among juveniles was constant, M^{juv}. Based on these assumptions, the proportion of males in year t, M_t, can be calculated from the proportion of males, M_{t-1}, and the reproductive success, B_{t-1}, (number of juveniles per female) in year t–1: $M_t = ((1 - M_{t-1})B_{t-1} \times M^{juv} / 2 + M_{t-1}) / ((1 - M_{t-1}) \times B_{t-1} / 2 + 1)$.

Lek size in relation to population size and proportion of first-year and adult cocks

The relationships between lek size and index of population size and between lek size and reproductive rates in the two preceding years were assessed with a normal linear model. The average lek size per region and year was used as outcome variable and the population index, the two reproductive rates (in the previous year and in the year before the previous year) and region were the explanatory variables. To assess whether the mechanisms that determine lek size differ between the two regions, we included all two-way interactions with region. Standard diagnostic residual plots were used to assess model assumptions.

Changes in the relationship between hunting bag and population size in the following spring

The correlation between hunting bag and the index of population size was measured with a normal linear model with population index as outcome variable and hunting bag as predictor variable. Both outcome and predictor variables were z-transformed before the model fit in order to transform the model coefficient into a Pearson's correlation coefficient. We included an interaction with year in order to measure how the correlation between hunting bag and population index changed over the years. We repeated this analysis with the first principal component of hunting pressure instead of year in order to measure how the correlation between hunting bag and population index changes with hunting pressure.

All statistical analyses were done with the software R ver. 3.3.1 (<www.r-project.org>). Statistical uncertainties such as standard errors and 95% credible intervals were based on the posterior distributions of the parameters of interest. The posterior distributions were obtained via Monte Carlo simulations assuming flat prior distributions using the function sim from the R-package arm (Gelman and Hill 2007).

Results

Population trends, hunting pressure and hunting bag

Changes in population size, hunting pressure and hunting bag are shown in Fig. 2. Population size fluctuated over the 36 years but did not show any trend. The index of hunting pressure shows a decline since 1988, with marked steps when the start of the hunting season was postponed in 1988 and the allowed number of cocks per hunter was reduced from 4 to 3 in 1991. A slight reduction of hunting pressure followed in 2000 when the number of hunting days was further reduced. Hunting bag showed an increase until 1990, followed by a decline.

Sex ratio of black grouse chicks

Over the whole study period 1981–2016 1264 male and 1299 female chicks were recorded in Northern Ticino (percentage of males 49.3%, 95%-CrI: 47.4 – 51.3%), 706 males and 848 females in Central/Southern Ticino (proportion of males 45.4%, 95%-CrI 43.0 – 47.9%). Over both regions, the percentage of males was 47.9% (46.3–49.4%). There was no clear trend over the years, the proportion of males among chicks showing an average increase of only 1.3% per 10 years (95% CrI: -0.5–3.2%). To summarize, the sex ratio of black grouse chicks was close to 1:1 over the whole study period.

Sex ratio of adult black grouse in relation to hunting pressure

The proportion of adult males showed a long-term increase from 1981 to 2016. For an average hunting pressure index and the mean year (1998) the estimated proportion of adult males was 33.5% (95% CrI: 32.3–34.8%) in Northern Ticino and of 29.4% (27.9–30.9%) in Central/Southern Ticino. The proportion of males was negatively correlated with hunting pressure (Table 2, Fig. 3). The model indicated a slight positive tendency over the years, which cannot be explained by the first principal component of hunting pressure.

If hunting had been stopped at the beginning of the study, the sex ratio would have changed rapidly. In the

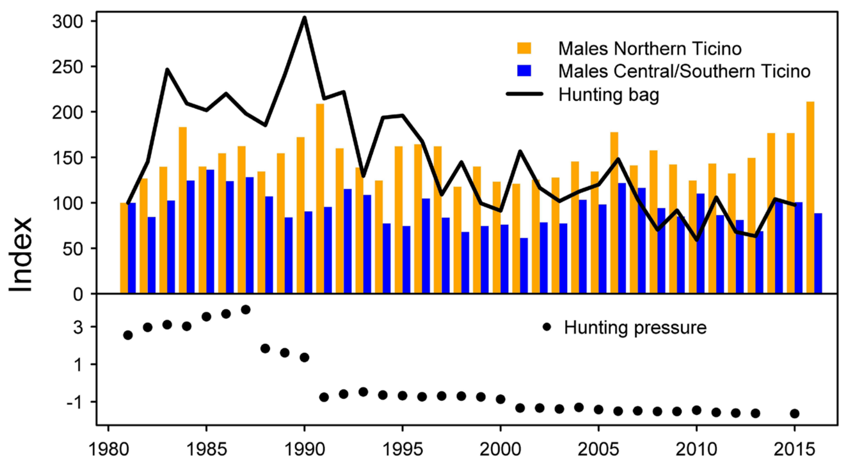

Figure 2. Indices of population size in spring (columns), of hunting bag (line) and of hunting pressure (dots) from 1981 to 2016.

Table 2. Estimated values of the model coefficients in the binomial model for the proportion of adult males with lower and upper limits of the 95% credible interval.

	Estimate	Lower limit	Upper limit
Intercept	–0.683	–0.740	–0.627
Region	–0.193	–0.282	–0.107
Hunting pressure (first principal component)	–0.090	–0.144	–0.035
Year (z-transformed)	0.070	–0.013	0.155

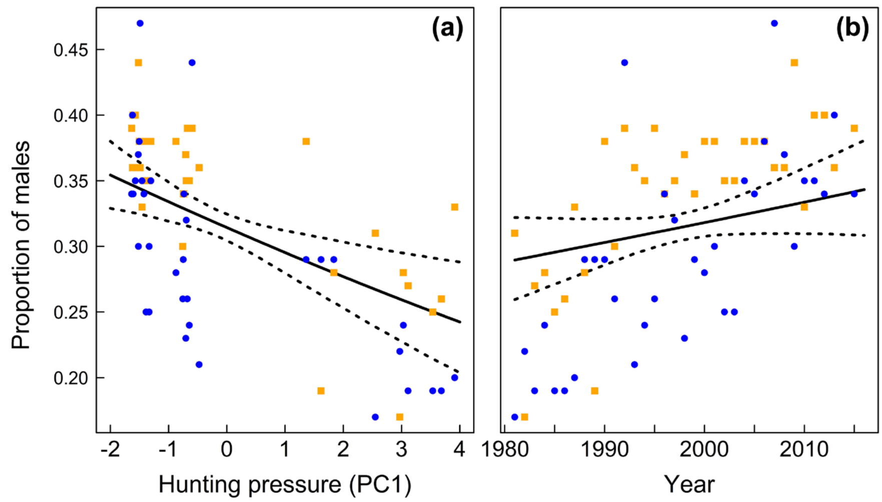

Figure 3. Partial effects of (a) hunting pressure (principal component 1) and (b) year on the proportion of adult males averaged over the regions. (a) shows changes in relation to hunting pressure independently of the year, while figure (b) shows changes over the years if hunting pressure had remained unchanged. Orange squares = Northern Ticino, blue dots = Central/Southern Ticino. The regression lines do not fit all points because partial effects of the variables assume a constant value of the other one.

study population the proportion of males at the beginning of the study period was only 23%. The model showed that without hunting the proportion of males rapidly approached 50% or 47.9%, respectively, for a scenario of 50% or 47.9%, respectively, males among chicks assuming equal survival between males and females (Fig. 4). The observed proportion of males also showed an increase in particular in the first years. It remained, however, much lower than what would be expected from the sex ratio among chicks, which indicates a lower survival rate of males.

Lek size in relation to population size and proportion of first-year and adult cocks

Over the 36 years 75% of a total of 4466 recorded display sites were used by single cocks, 14% by two cocks and only 11% by groups of 3–11 cocks. Out of 6734 cocks 50% were displaying alone, 18% in groups of two, and 32% in groups of 3–11 cocks. Lek size varied in relation to reproductive success in the two preceding years (Table 3, Fig. 5). Mean lek size per year was positively correlated with the index of population size. The correlation was stronger in Central/Southern Ticino than in Northern Ticino. Mean lek size in both regions was also negatively correlated with reproductive success (expressed as number of recorded chicks per total number of hens) in the preceding year. Effects of reproductive success in the preceding year (RR1) and two years before (RR2) differed (difference between the effects of RR1 and RR2, averaged over the two study regions: 0.085 95% CrI: 0.026–0.147; posterior probability of the hypothesis that RR2 has a more positive effect on lek size than RR1 was 0.997). In Central/Southern Ticino lek size increased over the years, independently of population size index and reproductive success of the preceding years), whereas it stayed constant in Northern Ticino.

Changes in the relationship between hunting bag and population size in the following spring

The correlation coefficient between hunting bag and population size index increased with increasing hunting pressure and showed a decline over the years (Fig. 6). In the period 1981–1999 population size in the following spring was strongly correlated with hunting bag in the year before, whereas in the second half of the study period no such relationship was found (Fig. 7).

Discussion

Our analysis showed that hunting affects population structure and presents indirect evidence that mortality due to hunting is additive. Harvest is a cause for the non-natural sex ratio among adults, as shown by the increase of the proportion of cocks due to the reduction of hunting pressure. The basis for the change in adult sex ratio is not a consequence of sex-specific mortality of chicks. High hunting pressure leads to lower number of cocks and as a consequence to smaller leks.

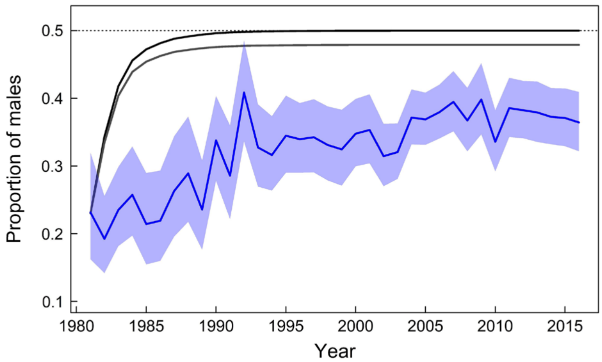

Figure 4. Observed proportion of males among adults per year (blue line with 95% CrI) and expected proportion of adult males if hunting had stopped given the following conditions: 1) the proportion of males among adults was 23% in year 1981, 2) the proportion of males among chicks did not change between years and was 50% (black line) or 47.9% (grey line), 3) survival of males and females does not differ, 4) survival of juveniles from an age of 4–6 weeks to the following spring is half as high as annual survival of older birds. With higher survival rates (see the highly variable data published so far: Caizergues and Ellison 1997, Baines 2007, Bowker et al. 2007) the modelled curves would even rise more steeply towards a proportion of 0.5 and 0.479 respectively.

If the sex ratio of chicks is balanced and mortality does not differ between sexes a sex ratio of around 1:1 can be expected among adults. This was the case in regions in the French and Swiss Alps without hunting (Ellison and Magnani 1985, Marti et al. 2016). A biased sex ratio among adult black grouse has, however, been observed in a harvested population in the French Alps, in which the percentage of males was only 30% (Ellison and Magnani 1985). To our knowledge, our study is the first providing evidence within the same study area that the low proportion of males is a consequence of hunting. The model showed how fast the sex ratio could approach a natural situation once hunting was stopped. The observed increase of the proportion of males in the first years of the study, when the strongest measures to reduce hunting pressure were introduced, is in line with these models. The rapid increase can be explained by the fact that in a situation with a low proportion of males, a large number of hens are available per cock, which produce an equal proportion of males and females. The observed increase of the proportion of males at the beginning of the study period, however, did not lead to an equal sex ratio, which indicates persistently lower survival rates of males. The model showed that the effect of hunting on sex ratio was somewhat reduced with the change in hunting pressure, but sex ratio was affected by hunting pressure throughout the whole study period. The analysis thus provides strong evidence that the mortality due to hunting is additive. The possible effects of environmental factors on sex ratio are considered negligible. Studies in Finland and Sweden showed that male black grouse chicks suffer a higher mortality than female ones if rearing conditions are bad (Lindén 1983, Hörnfeldt et al. 2001). The slightly lower percentage of males among chicks in Central/Southern Ticino where habitat quality is suboptimal compared to Northern Ticino points in the same direction. The deviance from a 1:1 sex ratio was however small (5%).

The question whether hunting mortality is additive or compensatory, has been studied with different methods and for a range of galliform species. Our approach, which is not based on individually marked birds, was made possible due to the marked changes in hunting pressure over the years and the fact that only cocks are hunted. Our results are in line with other studies on grouse. Bergerud (1985) concluded, based on an analysis of data from several studies with individually marked birds from several grouse species, that hunting was mostly additive. A study on radio-tracked ruffed grouse *Bonasa umbellus* concluded that mortality due to hunting was at least partially if not completely additive (Small et al. 1991). Willow grouse *Lagopus lagopus* were studied with the same methods in Sweden and Norway. In Sweden hunting mortality was also shown to be partially if not totally additive to natural mortality (Smith and Willebrand 1999). In an experimental study in Norway hunting mortality was partially compensated (Pedersen et al. 2004). A study on greater sage-grouse *Centrocercus urophasianus* came to the same conclusion based on lek counts (Connelly et al. 2003, Gibson et al. 2011). In an experimental study on bobwhite quail *Colinus virginianus*, with simulated hunting mortality by catching and removing birds in autumn/winter, mortality was additive as well. Without removing individuals winter survival rate was 47.9%, when individuals were removed survival decreased to 20.9% as expected from an additive effect of removal of individuals (Williams et al. 2004). Radio-tracked grey partridge *Perdix perdix* in the French Pyrenees suffered a monthly mortality rate of 5%, which increased to 30% during the main hunting period in October. According to the modelled growth rate population size remained stable without hunting but declined under the influence of hunting-induced mortality (Besnard et al. 2010).

Further evidence for a negative effect of hunting on population structure is shown by the observed relationship between

Table 3. Parameter estimates with 95% credible interval for the model of mean lek size.

	Estimate	Lower limit	Upper limit
Intercept	1.404	1.317	1.490
Year (z-transformed)	–0.014	–0.070	0.044
Index population size (z-transformed)	0.198	0.115	0.282
Reproductive success previous year (z-transformed)	–0.077	–0.134	–0.020
Reproductive success two years before (z-transformed)	0.019	–0.038	0.075
Region	0.270	0.132	0.411
Year × Region	0.125	0.037	0.205
Index population size × Region	0.102	–0.042	0.248
Reproductive success previous year × Region	0.028	–0.057	0.116
Reproductive success two years before × Region	0.008	–0.075	0.093

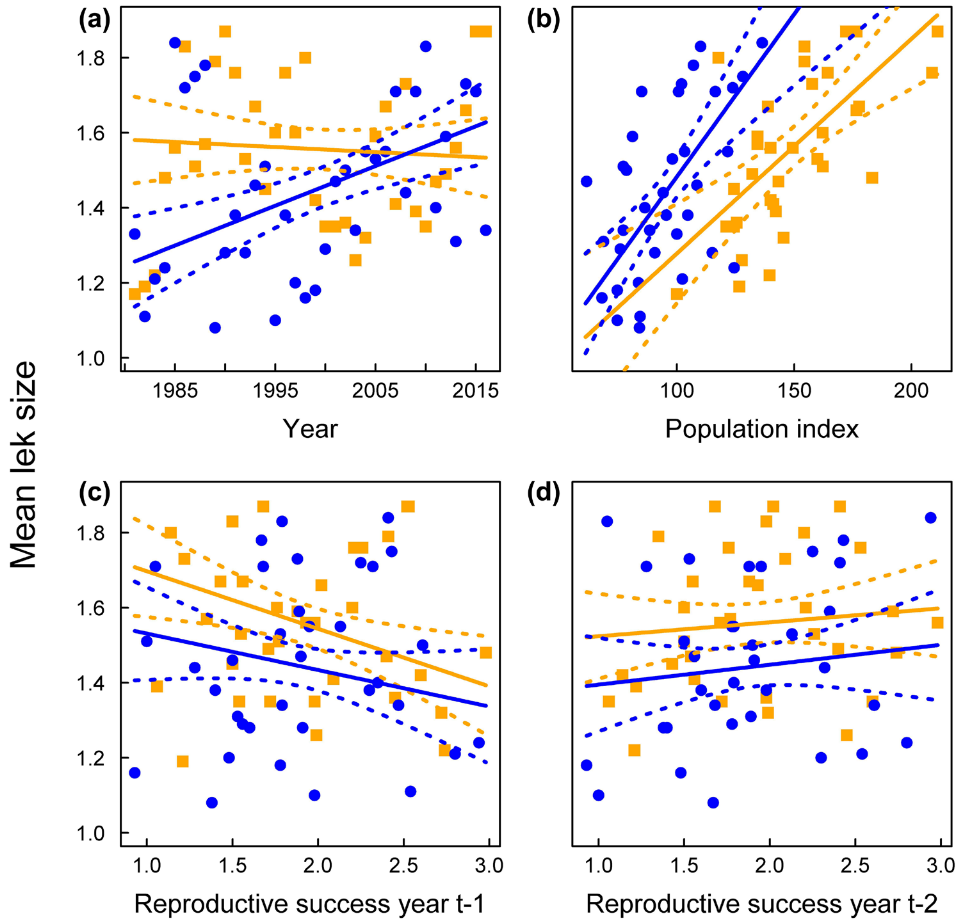

Figure 5. Mean lek size in relation to (a) year, (b) population size index of cocks, (c) reproductive success in the preceding year, and (d) reproductive success two years earlier. Points show raw data, lines show the partial effects of the variable for both regions (orange squares = Northern Ticino, blue dots = Central/Southern Ticino). Dotted lines show the 95% CrI. Partial effects show the effects of a variable under the assumption that all other variables are constant.

the size of leks and population size, which was also found in Finland (Koivisto and Pirkkola 1961) and in Italy (Nelli et al. 2016). The reduced density of cocks due to hunting leads to smaller leks, which affects the reproductive behaviour of black grouse as hens prefer to mate with males in larger leks (Alatalo et al. 1992). The high percentage of solitary displaying cocks in the Ticino is due to the locally low densities of cocks and further a result of a high percentage of young birds depending on the reproductive success in the year before, which was also found in a Swedish population (Höglund and Stöhr 1997). Leks on the other hand are usually formed by two-year old or older cocks (Kervinen et al. 2016).

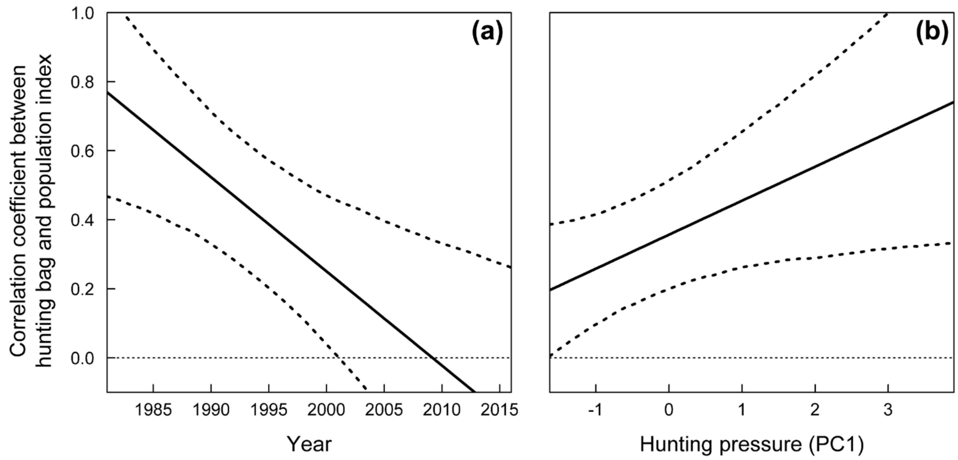

Figure 6. Correlation coefficient between hunting bag and population index in the following year in relation to (a) year and (b) hunting pressure (principal component 1 see Table 1).

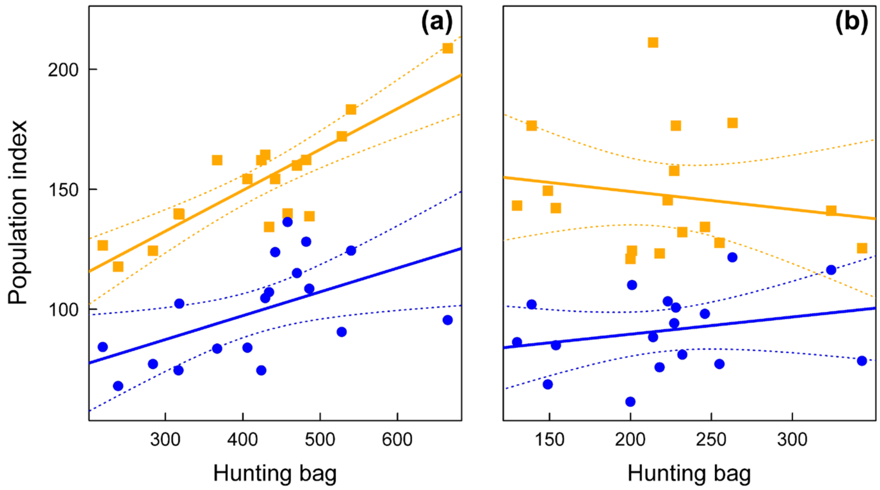

Figure 7. Population size index in relation to hunting bag (a) during the years 1981–1999, and (b) during the years 2000–2016 for the two regions (orange squares = Northern Ticino, blue dots = Central/Southern Ticino).

Non-selective hunting of cocks leads to smaller leks, which lowers the chances of females to choose the fittest males likely to make the most important contributions to the population (Kervinen et al. 2016, Koivisto and Pirkkola 1964). The preservation of large leks was therefore considered important for the stability of a population in Scotland (Geary et al. 2012). An increase of a population in the western Italian Alps over 25 years was accompanied at first by an increase in lek size and at a later stage by an increase of solitary cocks (Chamberlain et al. 2012). This might have been a result of an increase in the proportion of young cocks in the population.

Our results also indicate that the management of hunting pressure can reduce the negative effects of hunting. Under conditions of high hunting pressure (high number of hunting days and high bag allowance) hunting bag was driven by population size. When the number of hunting days was low and previously fixed to particular dates and hunting bag restricted to a small number of cocks hunting possibilities were mainly affected by weather conditions, which overall resulted in a lower hunting bag. A study of willow grouse in Sweden showed a similar effect of a reduction of hunting effort in order to minimise non-adaptive losses (Willebrand et al. 2011).

Over the 36 years mean population size of black grouse in our study area did not change but showed strong fluctuations. This is in contrast to many populations in Europe, which show declines, mostly related to insufficient reproductive output (Jahren et al. 2016). Even with no signs of a negative trend in the population the negative effects on population structure and mortality indicate that hunting of black grouse in our study area is problematic. It is likely that the negative effects shown limit population growth, yet a growing population would be desirable to improve the conservation status in a species which is likely to suffer from changes in land-use and climate in the future (Bollmann 2010). If for political and cultural reasons a complete hunting ban cannot be introduced, hunting management has to be continuously adapted to changes in the size and structure of the population as well as changes in habitat conditions. It is therefore essential to continue monitoring of population size and of demographic parameters. The hunting regulations introduced so far to reduce hunting pressure have shown a positive effect towards the target of reaching a natural population structure and should be continued and strengthened.

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