UNIVERSITÀ DEGLI STUDI DELL'INSUBRIA
Science and High Technology Department
Ph.D. program in Chemical and Environmental Sciences
XXX Cycle

ASSESSING ALPINE GALLIFORMS (AVES; GALLIFORMES) VULNERABILITY: MODELLING POPULATION TRENDS AND THREATS

Supervisor: Dott. Adriano MARTINOLI

PhD candidate
Alessio MARTINOLI

March 2018

Nullius in verba

ABSTRACT

This research work focused on the evaluation of population trends and conservation threats of three Alpine Galliforms species in Italy, namely Black grouse (*Lyrurus tetrix* L.), Alpine Rock ptarmigan (*Lagopus muta helvetica* Thienemann) and Alpine Rock partridge (*Alectoris graeca saxatilis* Bechstein). Despite being listed in Annex I and II of the Birds Directive 2009/147/CE and having unfavourable conservation statuses, to date the assessment of medium term national trends relied chiefly on extrapolations of local data to national scale, since a national survey scheme has not yet been implemented. Global change is predicted to severely affect species' conservation within the XXI century, but only few studies have analysed the role of land use/land cover changes in this context.

Based on these premises, I performed a first-ever assessment of a medium term trend of the three target species, exploiting all available data on annual counts and game bags, both as individual proxies and in an integrated fashion (Chapter 1 and Chapter 2). According to the results, the current IUCN conservation statuses of the Italian populations seem appropriate (LC for Black grouse, VU for Rock ptarmigan and Rock partridge; estimated population reductions from 1996 to 2014, respectively, -11%, -58%, -43%), although uncertainty on trends remained high, possibly influenced by different game management policies enforced in regions, which act on hunting pressure and census effort. However, the integration of counts and bags helped improving estimates precision and reducing bias by increasing sample size and averaging proxy-specific bias sources. No clear regional patterns emerged, except a W-E gradient in pre-Alpine Black grouse populations.

Subsequently, I showed that intensive land abandonment is likely to have caused the observed Black grouse negative trend in pre-Alpine areas (Chapter 3). The comparison of past and present land cover, also with the help of remote sensing techniques, revealed a massive habitat suitability loss in Central Alps (Lombardy region) from the early 1980s to present time, resulting from shrub encroachment and forest ingrowth, chiefly at lower elevations and in wood pastures. Habitat loss (-66% in the outer Alps, -23% in the inner Alps) was not compensated by gains at higher elevations, that occurred only marginally in the inner Alps.

Finally, I tested whether marginal grouse populations living in sub-optimal environments are characterized by ecological plasticity, which could help buffering predicted negative impacts of global

change (Chapter 4). This hypothesis was not confirmed for the Rock ptarmigan. Conversely, populations living in the core of the Alpine range exhibit more plasticity than marginal, exploiting a wider range of environmental conditions.

This PhD project led to an increase of knowledge of the conservation status of Italian Alpine Galliforms, with an in-depth analysis on factors affecting conservation of populations. I highlighted the need for a national survey scheme and national game management guidelines applied uniformly across the Italian Alps to improve the robustness of population abundances data in order to allow the elaboration of national management and conservation strategies on solid bases. Then, I recommend that habitat management measures should be implemented either to directly constrast the negative effects of land use/land cover changes or to indirectly compensate for climatic alterations.

INTRODUCTION

Biodiversity, global change and conservation biology

Since the UN "Earth Summit" held in Rio de Janeiro in 1992, which led to the enforcement of the Convention on Biological Diversity (CBD), biodiversity conservation has become a major theme in environmental policies worldwide. In 25 years, scientific knowledge of the role of biodiversity as key factor in regulating ecosystems and their equilibria increased as a result of an exponential growth of biodiversity-related research (Liu et al. 2011). Conservation biology, defined as "crisis discipline" by one of its founders Michael Soulé (1985), has become meanwhile an independent branch of knowledge, with a number of dedicated journals. It is a multidisciplinary science, which draws on several disciplines, including basic (e.g. physiology, genetics, ecology, biogeography) and applied sciences (e.g. natural resource management, hazard evaluation), as well as economics, law and social sciences. Its basis has been increasingly embedded into land management, agricultural and energetic policies.

Focal aspects of conservation biology are the assessment of species population trends, the evaluation of the drivers of population dynamics and changes in abundance and distribution, the study of community-related effects, the quantification of diversity and its variation from genetic to ecosystem scale, the prediction of future scenarios. Each of these topics can be approached from a different spatial and temporal resolution. On a geographic basis, the research scope may range from single populations with limited distribution to global diversity studies, while with regard to time, the analysed period mostly depends on the length of available time series. Usually, spatial and temporal resolution are inversely correlated; data on single population abundance, or its proxy, may start in the 19th century, while the first global diversity assessment dates back to the end of the 20th century (Watson and United Nations Environment Programme 1995). Most valuable research comes where the two contrasting issues meet, that is, at the wider spatial and longer temporal scale (Henle et al. 2014). Nevertheless, specific questions may be answered only at smaller scales with a finer resolution and possibly mechanistic explanation of the observed phenomenon. The major threats to biodiversity have been identified with the help of conservation biology, both as direct drivers (habitat degradation, fragmentation and loss, invasive alien species, climate change, pollution, over-exploitation) and indirect drivers (demands for food and energy, energy, which ultimately derive from increasing exploitation of natural resources), with uneven impacts between rich and poor countries (Soulé 1991; Secretariat of the Convention on Biological Diversity 2014). However, local and global conservation strategies outcomes have been a mix of successes and failures, with a significant gap between proposed and implemented conservation actions (Hayward 2011).

Biodiversity loss is identified as the most crucial aspect of global change; the current extinction rate, estimated as 100 to 1000 times higher than the basal natural rate, has overshot well beyond the "planetary boundaries" associated with the Earth's biophysical processes that guarantee a "safe operating space" for mankind (Rockström et al. 2009). In fact, the "move, adapt or die" paradigm of biogeography is concerning all plant and animal taxa across different regions of the world at the same time (Thomas et al. 2004) and the speed at which species will be able to shift their niches in time, in space or physiologically will determine winners and losers (Bellard et al. 2012).

The Alpine biodiversity

The Alps represent a continuum of different ecosystems from sub-Mediterranean scrubs to high tundra vegetation, enclosing the equivalent of thousands of kilometers of latitudinal gradient at a small geographical scale. Hence, the Alps are considered a biodiversity hotspot (Körner and Spehn 2003). Annex I of the Habitats Directive (92/43/EEC) lists in total 198 habitat types of which 100 Annex I habitat types are found in the Alpine region. Vascular plant flora comprises more than 4500 species, a figure equivalent to about 40% of the native flora of Europe (Ozenda 1985), albeit sharing only 2% of the continental area. Endemic species represent 10% of the flora (Theurillat 1995). Fauna is estimated counting more than 30000 species (Chemini and Rizzoli 2003).

Geographic, geologic, geomorphologic, biogeographic, climatic and anthropogenic factors contribute to the observed high richness of species. The Alps are centrally located in the European continent, sharing elements of several biota whose distributions often meet there. For example, a substantial percentage of the Swiss flora is present in other mountain ranges or even other continents (Sierra Nevada 35%, Central Pyrenees 65%, Scandes 46%, Ural 24%, Altai 31%, Caucasus 29%, Himalaya 29%, Ozenda 1985). Being Alps a relative recent range that originated in the Late Mesozoic, ecosystems are distributed along steep slopes, which determine a sharp climatic gradient. High alpine species are exposed to the same ecological conditions which can be found in the sub-Arctic, nonetheless possibly surrounded at close distance by thermophilous broadleaf forests, which occupy lower elevations. Local geomorphologic conditions (aspect, slope, terrain roughness) further enhance climatic diversity by determining the existence of different microclimates. Soils biogeochemistry is influenced by climatic conditions and by the different substrata that can be found in the Alps, which have a central backbone of crystalline rocks and external fringes of limestone and schist. This promotes plant diversity, both alpha (species) and sub-alpha (genetic, hence, for plants, ecotypes), by means of ecological vicariance. From the biogeographic standpoint, a number of species across animal and plant taxa show a so-called "Arctic-Alpine distribution" resulting from glacial and interglacial events that occurred in the Quaternary, which determined rapid and extensive distribution shifts north-southwards, with population isolations followed by subsequent recolonizations (Habel and Assmann 2009). The Alps played an important role in the course of this process acting as refugia throughout several glacial cycles and currently host many cold-adapted species for which they usually represent their foremost and often disjoint population. Finally, man has shaped the Alpine environment for centuries exploiting natural resources for food, timber, stones and, more recently, for energy and recreation. Human settlements in the Alps dates back to the Mesolithic (Scoz et al. 2016), but only in the last centuries did landscape markedly change because of anthropogenic actions. A certain part of the biodiversity of the Alps is therefore linked to semi-natural environments and to traditional land-use. Biodiversity benefitted from increased structural heterogeneity in the resulting cultural landscape, especially below the treeline where most grasslands are of anthropic origin. The plant species diversity of these grasslands is estimated being 3 times higher than in the forests they replace (Fischer et al. 2008).

Global change and Alpine biodiversity

Climate change

The effects of climate and land use changes are clearly detectable on Alpine biodiversity from a vast scientific literature that has addressed this issue in the past 40 years. First reports of warming-induced species upward shifts date back to the early 20th century (Klebelsberg 1913), subsequently confirmed as increase of species richness at high elevations (Braun-Blanquet 1958; Grabherr et al. 1994; Walther et al. 2005; Parolo and Rossi 2008). A response of vegetation to climate warming has been evidenced in different aspects of plant ecology, such as species distribution (Dirnböck et al. 2003), composition of communities (Pauli et al. 2007; Gottfried et al. 2012), vegetation structure (Dullinger et al. 2003), species phenology (Moser et al. 2010) and ecosystem productivity (Zweifel et al. 2010). With respect to species distribution, several different possible shift patterns along the elevational gradient related to climate change were identified by Maggini et al. (2011), including leading edge expansion, trailing edge retraction, optimum shift, range shift and change in abundance. The first pattern has been detected in 33 out of 95 Alpine birds species in Switzerland (Maggini et al. 2011), but also invertebrates have been shown to track climate warming by expanding range towards higher elevations (Juillerat 2005). Nevertheless, elevational shifts are far from being a universal species response, as lack or weak upward movements have been shown for other plant and animal species (Archaux 2004; Popy et al. 2010; Cannone and Pignatti 2014). The increase of extreme weather events, such as heat waves, drought or heavy rains affects populations fitness through recruitment failure, reduced survival or physiological alterations on individuals (Gehrig 2006; Jonas et al. 2008; Larcher et al. 2010). However, a certain degree of ecosystem resilience helps delaying the effects of climate change at community level (Menéndez et al. 2006; Devictor et al. 2008). A remarkable amount of research has been focusing on predicting the response of communities depending on future climatic scenarios. Consequences expected by the end the 21st century include species turnover, local extinctions and biodiversity loss (Settele et al. 2008; Pearman et al. 2011; Chamberlain et al. 2013; Maggini et al. 2014).

Land use change

At the same time with the observed warming, in the last few decades changes in society and agricultural production methods have led to substantial changes in land-use systems and abandonment of traditional practices across the whole Alpine chain. This dynamic is an aspect of the so-called LULCC (‘land use/land cover changes’), which are an essential part of the wider global change scenario (Meyer and Turner 1994). Indeed, the Alpine landscape was shaped for centuries by agricultural activities that led to diverse ecosystems with high levels of biodiversity (Tasser and Tappeiner 2002), especially along forest-meadows ecotones, which ultimately were markedly shaped by cattle grazing and hay mowing. The vegetation succession following abandonment of traditional practices resulted in a structural change from open to closed landscape and from high to low patchiness, with reduction of the ecotonal environment and habitat heterogeneity. Negative effects of the decline of traditional farming that is been occurring since the mid-20th century are recorded across different taxa inhabiting open and semi-open habitats (Dirnböck et al. 2003; Laiolo et al. 2004; Settele et al. 2008; D'Amen and Bombi 2009; Zimmermann et al. 2010; Koch et al. 2015). Treelines are temperature-controlled boundaries (Körner and Paulsen 2004), but historically man contributed to move their elevation 150-300 m lower (Holtmeier and Broll 2005; Wallentin et al. 2008). Subsequent to land abandonment, treelines are currently climbing to higher elevations filling the gap with their potential climatic position (Gehrig-Fasel et al. 2007). Climate change interacts with land abandonment by accelerating the recolonization of woody vegetations especially at lower elevations, providing more favourable conditions for shrubs and trees growth (Bolli et al. 2007; Leonelli et al. 2011; Boulangeat et al. 2014; Tasser et al. 2017), but at short time scale most of the observed upward shift of treelines is attributed to a gap-filling process and temperature increases only play a marginal role (Gehrig-Fasel et al. 2007; Kulakowski et al. 2011). Indeed, treeline position is believed to lag behind climatic changes by at least 50 years, due to recruitment lags, slow tree growth and competition with faster-growing shrub layer (Dirnböck et al. 2003; Harsch et al. 2009; Körner 2012). Increase in forest cover and density causes also a positive feedback by limiting the effect of avalanche disturbance, which represented a major driver of forest structure and treeline position enhanced by human deforestation in previous centuries (Kulakowski et al. 2011; Bebi et al. 2017). In turn, the decline in avalanche frequency was shown to increase the relative importance of climatic stress at the treeline (Kulakowski et al. 2006).

Recreational activities

The Alps represent also a major global tourism destination, with an estimated 120 million overnight stays per year (Permanent Secretariat of the Alpine Convention 2010). Ski resorts have been created in many parts of the Alps since the early 20th century, making ski-tourism an important economic activity, providing 10-12% of the jobs in the region (Agrawala and Organisation for Economic Co-operation and Development 2007). The area converted into ski-runs has still increased recently (Abegg et al. 2007), despite the threat of an upward shift of the snowline and the duration of snowcover caused by climate change (Elsasser and Messerli 2001; Abegg et al. 2007; Durand et al. 2009; Beniston 2012) and the consequent severe economic impact predicted for the next decades (Meier 1998; Unbehaun et al. 2008). Winter sports, are threatening Alpine biodiversity due to habitat fragmentation and degradation from ski-related urban development and direct human disturbance to wildlife and vegetation (Rixen and Rolando 2013; Sato et al. 2013), a conflict that is predicted to intensify in the future due to climate change (Brambilla et al. 2016). Reduced diversity caused by ski runs has been detected in various taxa, such as orthopterans (Negro et al. 2010; Keßler et al. 2012), dipterans (Haslett 1997), coleopterans (Negro et al. 2009, 2010), mites (Baratti et al. 2000), spiders (Negro et al. 2010), small mammals (Negro et al. 2009; Rehnus et al. 2014) ungulates (Hamr 1988) and birds (Laiolo and Rolando 2005; Rolando et al. 2007; Arlettaz et al. 2007; Patthey et al. 2008), as a result of skiers disturbance, landscape fragmentation, soil perturbations and artificial snow-making. Vegetation structure and composition are affected by ski runs management likewise, resulting in lower plant species diversity (Wipf et al. 2005).

Alpine Galliforms conservation threats in changing environments

Alpine Galliforms are bird species belonging to the pheasant family (Phasianidae). In the Alps 5 species are found, 4 belonging to the grouse subfamily (Tetraoninae, i.e. Black grouse *Lyrurus tetrix* L., Capercaillie *Tetrao urogallus* L., Alpine rock ptarmigan *Lagopus muta helvetica* Thienemann, Hazel grouse *Tetrastes bonasia* L.) and one to the partridges and francolins subfamily (Perdicinae, i.e. Alpine rock partridge *Alectoris graeca saxatilis* Bechstein) (del Hoyo et al. 2017). Common traits are found in a mostly ground-dwelling lifestyle, a lack of a proper migrating behaviour - albeit winter displacements are observed within the range of few tens of kilometers or few hundred metres in elevation (Ellison et al. 1989; Bernard-Laurent 1991) - and a diet largely based on plant material, with specific adaptations of the digestive system, such as the presence of a well-defined crop, a muscular gizzard and very long caeca.

Grouse and Rock partridge have different biogeographic histories and ecological requirements only partly overlapping. The formers are boreal species that underwent peripatric speciation from a common western Nearctic ancestor (Drovetski 2003), whose Alpine populations represent in fact the marginal fringe of a wide Euro-Siberian distribution. Quaternary glaciations influenced grouse distribution on the Alps, especially the Rock ptarmigan, which has a disjoint Arctic-Alpine range. Genetic evidences show that Black grouse Alpine populations derive from several southwards distribution shifts following different glacial pulses events (Caizergues et al. 2003b) while Capercaillie and Hazel grouse isolation from the main core of their distribution is the consequence of extinction of lowland populations that once inhabited Central Europe, caused by anthropogenic landscape transformations (Segelbacher and Piertney 2007). Grouse have specific eco-ethological and anatomical adaptations to cold climates common to all species, albeit some anatomical features are more prominent in *Lagopus spp.*, which lives in the harshest environments among grouse, or in Siberian/Fennoscandian populations (Potapov and Sale 2014). In all grouse tarsi are feathered to the base of the toes, except for *Lagopus spp.*, in which also toes are completely feathered, to insulate hind limbs from cold and to improve buoyancy while walking on snow. Similarly, nostrils are feathered to reduce heat dissipation and toes have horny pectinates along the sides, a feature that is considered an adaptation to digging snow burrows. In fact, grouse are able to withstand boreal and Alpine winters also by roosting in snow burrows, where temperatures can be up to 40°C higher than the ones found outside the snow cover (Marjakangas et al. 1984). The proportion of the day spent in burrows is inversely proportional to the temperature (Marjakangas 1986). In the Alps, where climate is milder than Siberia or Fennoscandia and snow is usually less powdery, birds often roost perching in trees during the night (Bocca et al. 2013).

Rock partridge, conversely, is an endemic species of Central Mediterranean mountain ranges, thus has a much more limited global distribution and lacks of specific behavioural and anatomical adaptations to cold climates. Hence, populations nesting at high elevations, sometimes in syntopy with Rock ptarmigan, in winter are forced to move at mid-elevations to avoid persistent snow cover (Lüps 1980, 1981, 2004).

All 5 Alpine Galliforms belong the small group of 11 species listed both in the EU Birds Directive 2009/147/CE Annex I (priority species) and Annex II (huntable species). Hence, management strategies of these species need to integrate both socio-economic aspects and conservation targets. Obtaining robust data and reliable models on population dynamics to achieve conservation goals, allowing a sustainable exploitation at the same time, is essential. According to the IUCN, none of these species is globally threatened, Rock partridge being an exception (classified as Near Threatened - NT, BirdLife International 2016). Nonetheless, their Alpine populations are locally declining or have shown recent distribution shrinkage, so national red lists classify them from Least Concern (LC) to Critically Endangered (CR, Capercaillie in Germany, Südbeck et al. 2007), depending on the species and the state. **Table A1** summarises the classification of the conservation statuses according to national and international red lists.

Table A1 - *IUCN classifications of Alpine Galliforms species at various scales. Species abbreviations: BG, Black grouse; CAP, Capercaillie; HG, Hazel grouse; PTA, Rock ptarmigan; PAR, Rock partridge. Conservation status abbreviations: LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endamgered; R, rare; np, not present. Sources: Global: BirdLife International 2016; Europe and EU27: BirdLife International 2015; FR: UICN France, MNHN, LPO, SEOF & ONCFS 2011; IT: Peronace et al. 2012; CH: Keller et al. 2010; AUT: Zulka 2005; DE: Südbeck et al. 2007; SLO: BirdLife International 2015.*

	GLOBAL	EUROPE	EU27	FR	IT	CH	AUT	DE	SLO
BG	LC	LC	LC	LC	LC	NT	NT	EN	increase
CAP	LC	LC	LC	VU	VU	EN	VU	CR	decrease
HG	LC	LC	LC	VU	LC	NT	NT	EN	decrease
PTA	LC	NT	VU	LC	VU	NT	LC	R	decrease
PAR	NT	NT	VU	NT	VU	NT	VU	*np*	fluct./ decrease

Table A2 - *Main threats to Alpine Galliforms species, in a scale from 0 (no threat) to 3 (major threat). Modified from Chamberlain et al. 2016. Species abbreviations: BG, Black grouse; PTA, Rock ptarmigan; PAR, Rock partridge.*

Species	Land aband.	Climate change	Energy	Forestry	Grazing	Hunting	Leisure	Urbaniz.
BG	2	2	0	2	2	1	3	3
PTA	0	3	0	0	2	3	3	3
PAR	2	2	0	0	2	3	3	3

Black grouse, Rock partridge and Rock ptarmigan were identified as the 3 most threatened species out of 69 Alpine birds according to a panel of 19 experts interviewed by Chamberlain et al. (2016). Among the 8 threats evaluated, only 'energy' ('*developments in renewable energy such as wind turbines, hydroelectric power*') and 'forestry' were considered of minor importance, while all other 6 received high scores, especially 'climate change', 'leisure' and 'urbanization' (**Table A2**). Hereinafter

I reviewed the literature that treated more specifically some of these threats in relation to Alpine Galliform conservation.

Distribution and population size

As stated before, Alpine Galliforms populations represent just a fraction of their European populations. Each species is estimated counting a few tens of thousands of individuals in the Alps (Black grouse, 55000-75000 displaying males; Capercaillie, 11000-17000 displaying males; Hazel grouse, 30000-55000 breeding pairs; Rock ptarmigan, 30000-50000 breeding pairs; Rock partridge, 11000-19000 breeding pairs; BirdLife International 2015a).

Alpine grouse populations live at the edge of species distributions, which is an intrinsic element of vulnerability, as marginal and isolated populations are considered more vulnerable to decline and extinction than core populations (Purvis et al. 2000). More specifically, in Alpine grouse reduced gene flow and genetic drift is further enhanced by limited post-natal dispersal and high philopatry that is characteristic of the subfamily (Martin and Hannon 1987; Caizergues and Ellison 2002). A genetic fingerprint of population fragmentation and isolation was detected on Black grouse, whose Alpine populations show low genetic diversity, measured as observed heterozygosity, expected heterozygosity and allelic richness, compared to Fennoscandian populations, where effective population size is remarkably higher (Caizergues et al. 2003b; Höglund et al. 2007). Isolation-by-distance was detected in Rock ptarmigan (Caizergues et al. 2003a), Capercaillie (Segelbacher and Storch 2002), and Hazel grouse (Rózsa et al. 2016), favoured by the presence of mountain ridges that act as barriers to dispersal (Segelbacher and Storch 2002; Kormann et al. 2012). However, Alpine Rock ptarmigan populations show higher genetic variability and higher allelic richness compared to Scandinavian and circumpolar populations (Collini 2011), likely resulting from the process of post-glacial recolonization from southern refugia (Hewitt 2004).

Rock partridge has instead a restricted worldwide range, which is an element of vulnerability as well. Moreover, it was shown that the species have lost variability through past population declines, and did not expand recently (Randi et al. 2003).

Climate change

Grouse are boreal/sub-arctic species well-adapted to live in cold climates, and are among the species able to withstand the harshest Siberian winter cold spells (Andreev 1999). Hence, climate warming is expected to induce direct and indirect negative effects on the species. Among direct effects, temperature rising beyond a certain threshold in summer limits Rock ptarmigan activity and feeding, which was observed selecting fresh microclimates in the shade (Visinoni et al. 2014). In the Swiss Alps, its distribution is confined to areas where mean July temperatures are below 10-12° C (Revermann et al. 2012). In fact, according to the 'heat dissipation theory' (Speakman and Król 2010) endothermic animals are limited by the ability to dissipate body heat rather than by the competition for a limited energy supply. For example, in Neartcic White-tailed ptarmigan (*Lagopus leucura* Richardson) panting seems to be triggered by temperatures beyond 21° C (Johnson 1968). Breeding success was shown to be negatively affected by precipitations and extreme weather events in spring-summer (Bernard-Laurent and Léonard 2000; Novoa et al. 2008; Barnagaud et al. 2010), a climatic feature whose frequency is expected to increase in the future (Beniston et al. 2007). Galliform chicks are not able to fully thermoregulate until they are 8–10 days old, so they are susceptible to cold and relatively high humidity (Boggs et al. 1977). Population dynamics seem influenced as well by changes in autumn-winter weather conditions. Delayed snow cover in autumn raises predation risk for Rock ptarmigan causing a mismatch with plumage (Imperio et al. 2013). Extreme winter conditions (cold/wet or warm/dry) negatively affect breeding success in the following summer, presumably by altering hens conditions, which either allocate more energy to survival than to reserve storage or become more exposed to predation or night chill if snow layer is too thin or absent, preventing the use of snow burrows (Barnagaud et al. 2010; Viterbi et al. 2015), a feature observed also in White-tailed ptarmigan (Wang et al. 2002).

As indirect effect of climate change, trophic resources get altered, reducing individual fitness. In fact, inclement weather may reduce the availability of arthropods or cause a mismatch with hatching, resulting in poor chick growth and increased mortality (Erikstad and Andersen 1983; Ludwig et al. 2006; Wegge and Kastdalen 2008). Moreover, food supplies and quality may be severely affected by an increase of secondary metabolites stored in food plants, hence affecting hen fitness and consequently limiting breeding success (Selås et al. 2011; Forbey et al. 2013). Another indirect effect is a potential increase in parasite diseases outbreaks related to extreme climatic events, favoured by a reduction in arrested larval stages, which eventually may cause large-scale synchronization of parasitic infections and, therefore, of population fluctuations (Hudson et al. 2006).

A major consequence of climate change on Alpine Galliforms is an elevational upward distribution shift, both observed and predicted (Revermann et al. 2012; Zurell et al. 2012; Pernollet et al. 2015), although lack of response was also detected locally (Novoa et al. 2016). Distribution shifts caused by climatic warming is unidirectional and follows the temperature gradient. This defines within populations distribution a leading edge at higher elevations and a trailing edge at lower elevation (Pernollet et al. 2015). Elevational shifts of Alpine populations are ecologically equivalent to north-eastwards latitudinal shifts predicted for Fennoscandian populations (Elmhagen et al. 2015) and, more generally, at continental scale (Huntley et al. 2006, 2007). Range upward shifts necessarily imply a distribution shrinkage at medium-long term, as the relative proportion of land decreases with elevation, and possibly determine increased isolation of populations. This represent a major threat especially for Rock ptarmigan, which already lives at high elevations. The lack of shift observed in some pre-Alpine Swiss populations may be linked to the fact that the species already lives at the edge of suitable environment, as mountain ranges locally do not pass 2500 m (Pernollet et al. 2015).

An open question is whether Alpine Galliforms are able to buffer negative effects of climate change through a certain degree of ecological plasticity, as it has been observed in other birds species in Europe, which were shown to have partially adapted some life-history traits or breeding phenology to increasing temperatures and seasons onset shifts (Nussey et al. 2005; Charmantier et al. 2008; Both and Visser 2011). In Finnish Black grouse populations, lekking behaviour is reported having advanced in the past four decades, resulting in a shift in hatching dates (Ludwig et al. 2006). However, breeding phenology of Rock ptarmigan populations in the French Alps and Pyrenees seem not to track climate change likewise (Novoa et al. 2008).

Land use changes

Subalpine areas are currently undergoing an unprecedented land abandonment, that is progressively causing loss of semi-natural elements of the cultural landscape. Farming discontinuation and forest expansion is considered the most relevant land use/land cover change in Italy in the second half of the 20th century (Piussi and Pettenella 2000), with an estimated 800,000 ha of pastures and hay meadows abandoned in the Italian Alpine slope during this period (Chemini and Giannelle 1999). In

Switerzland, forested area has expanded by one third from 1850 on, mostly as natural regrowth on abandoned agricultural land (Mather and Fairbairn 2000; Gellrich et al. 2007). This phenomenon in the pre-Alps occurred much faster than in the inner Alps, favoured by warmer and wetter climate and mainly lead by broadleaved, faster growing species (Piussi and Pettenella 2000). In Italian pre-Alps, traditional farming abandonment started in the 1950s, whereas in the inner Alps farming activities declined to a minor extent (Della Marianna et al. 2004).

Densification of woody vegetations are detrimental to Black grouse, since a balanced mosaic of trees, shrubs and grassland is necessary for food and cover of chicks (Magnani 1988; Patthey et al. 2012; Braunisch et al. 2016). The process is mainly driven by tall shrubs as the Green alder (*Alnus viridis* (Chaix) DC) and the Dwarf mountain pine (*Pinus mugo* Turra) and dwarf shrubs as Rhododendron (*Rhododendron spp.* L.) and Junipers (*Juniperus spp.* L.). In particular, Green alder, which traditional farming and agricultural activities confined to steep slopes and avalanche tracks, has spread on wet and nitrogen-rich meadows, with detrimental effects on arthropod biomass availability to Black grouse chicks (Anthelme et al. 2001). Food availability is crucial for Black grouse chicks survival. Being a ground-dwelling precocial species, chicks have extremely high energy requirements, which lead them to a 30-fold body mass gain in 6 weeks, supplied by intensive foraging sessions on arthropods (caterpillars, ants, spiders, grasshoppers, bugs) (Ponce 1992; Signorell et al. 2010). Dwarf shrubs are important features in Black grouse habitat as they provide quick shelter from predation, which represent the major cause of grouse chick mortality (Hannon and Martin 2006), but when shrub/meadow cover ratio is high, they become an impediment to foraging movements and limit invertebrate availability. The optimal breeding habitat results therefore from a trade-off between food abundance and predation risk, in which none of meadow/shrub/forest layers should cover more than 50% (CREN Rhône-Alpes 2009). Land use changes have already lead Germany lowland Black grouse populations to the verge of extinction causing a dramatic decline from the 1950s to the 1970s (Ludwig et al. 2008, 2009b, 2009a).

Also Rock partridge is likely to suffer from land abandonment, although fewer studies have directly addressed this issue on the Alps. In particular, hay meadows located at mid- or low elevations were intensively used by the species as winter quarters (Lüps 1980, 1981), given that the species avoids snow cover and lacks specific adaptations to cold, unlike Rock ptarmigan (Lüps 2004). Disappearence of this habitat was considered a major driver of observed population reductions in the 1970s-1980s

(Spanò and Bocca 1988; Brichetti 1990; Bernard-Laurent and De Franceschi 1994; Meriggi et al. 1998; Cattadori et al. 2003b). Similarly, land abandonment was shown as a major cause of population declines and isolation also in the Apennines, inhabited by the subspecies *A. g. graeca* (Rippa et al. 2011; Sorace et al. 2013a).

Being Rock ptarmigan a species that strictly avoids wooded areas, treelines shifting upwards resulting from the above-mentioned “gap-filling” process (Gehrig-Fasel et al. 2007; Leonelli et al. 2011) is predicted to reducee the species available habitat to 50% by the end of the 21th century (Ferrarini et al. 2017), enhancing the displacement in elevation caused by climate change and eventually increasing the species vulnerability (Maggini et al. 2014). A 50% reduction in the area used by Rock ptarmigan in long-term study site in the Central Swiss Alps was already seen in a 45-year period from 1970 to 2015, mainly caused by invasion of Arolla pine (*Pinus cembra*) into former meadows (Marti et al. 2016).

Nevertheless, abandonment of grazing activities may have a positive effect in the first stages of the vegetational succession, as it has been shown in Hazel grouse, for which spontaneous reforestation of pastures is assumed to have triggered the recently observed southwards range expansion in the French Alps (Montadert and Leonard 2003), and in Black grouse, whose expansion in Italian central pre-Alps in the 1960s is attributed to land abandonment likewise (De Franceschi 1994).

However, even if cattle grazing was largely responsible for the maintenance of structural vegetation heterogeneity in Alpine cultural landscape, early arrivals in the subalpine pastures at the onset of June may cause brood failures and nest destructions. Moreover, herds are often kept by wandering shepherd dogs that may threaten incubating hens (Rotelli 2014). In France, specific projects to favour the coexistence of pastoral activities and Galliform presence have been implemented (Losinger et al. 2011; Maillard et al. 2012).

Disturbance from recreational activities

Leisure activities have been increasingly being considered in the last decade as threat to Alpine Galliforms conservation, both as indirect (ski piste creation and management) and direct effects (off-piste skiing, walking, biking, rock climbing etc.) with quantitative assessments of disturbance effects. Physiological (stress and energetics), behavioural (activity budget) and demographical (densities) responses of Black grouse to winter sports are heavily influenced by the presence of ski resorts and off-piste skiing (Arlettaz et al. 2007, 2013). Wintering grounds were less frequently used or even abandoned in the presence of snowsports, with ski-resorts and the associated ski-tourism having a stronger impact than off-piste activities (Braunisch et al. 2011). However, off-piste skiing is correlated to higher concentrations of faecal stress metabolites in Black grouse and Capercaillie, suggesting that this activity may be detrimental to birds' fitness in a season with higher energy budget constraints (Baltic et al. 2005; Arlettaz et al. 2007; Thiel et al. 2011; Formenti et al. 2015). In addition, the density of Black grouse cocks displaying is lower close to ski resorts and hiking trails with respect to natural undisturbed habitats (Patthey et al. 2008; Immitzer et al. 2013).

Hybridisation

Cases of hybrids between grouse species are reported occurring rather frequently, so that they have specific names in many languages (e.g. male Black grouse x Capercaillie hybrid is known as *Rackelhuhn* in German, *Mejnak* in Russian, *Tetraone mezzano* in Italian), but this is a natural phenomenon whose prevalence is still very low and does not affect conservation, even if hybrids are fertile (Potapov and Sale 2014). Conversely, hybridization is considered a threat to Rock partridges conservation, as declines in late 20th century in most of their native range used to be compensated by massive releasing of captive-reared Chukar partridges (*Alectoris chukar* Gray), with whom Rock partridge hybridises (Randi et al. 2003). Thus, the genetic integrity of the species might be at risk of widespread introgressive hybridisation which may disrupt local adaptations in natural Rock partridge populations (Bernard-Laurent et al. 2001; Barilani et al. 2007).

Hunting

Grouse have long history as game birds throughout all Europe since the Middle Ages and before (Storch 2007) and hunting is still practiced also on the Alps in accordance with the prescriptions of the Birds Directive. The long-lasting debate on whether hunting mortality should be considered additive or compensatory to natural mortality (Nichols et al. 1984; Lebreton 2005) has concerned also Galliforms, albeit almost all studies focused on Fennoscandian or Scottish populations, or Nearctic species (Anderson and Burnham 1981; Ellison 1991; Sandercock et al. 2011). In the 19th century overhunting was believed to have occurred and to have led to population reduction (Giglioli

1891; Arrigoni degli Oddi 1899). Hunting statistics started being recorded in the second half of 20th century, but the lack of corresponding data on hunting effort, of independent standardised surveys and of the gradual enforcement of hunting limitations make it difficult to evaluate a possible overhunting in this period (Cattadori et al. 2003a). However, evidence of overexploitation of populations without harvest restrictions was shown in Southern Switzerland for the Black grouse from the 1960s to the 1980s (Zbinden and Salvioni 1997), showing that inadequate harvest planning may have detrimental effects on species' conservation. Reliable monitoring schemes with data on current stocks and annual reproductive success can minimise this problem (Ellison 1991) and are currently enforced in all Alpine countries. Poaching has been reported most frequently from regions with poor rural economics (parts of Asia and eastern Europe), but also from some regions that combine relatively poor law enforcement with a high trophy or sport value of grouse, as the Alpine region (Storch 2000, 2007). Spring hunt of displaying Capercaillie and Black grouse males at the leks, which is traditional in Austria, involves a high risk of disturbing the social system at the lek, and may result in reduced reproductive success (Klaus et al. 1989, 1990). However, this hunting type has been considered a violation to the Bird Directive and Austria was pursued in 2007 with an infringement procedure.

Table A3 *– Average annual national bags. Species abbreviations: BG, Black grouse; CAP, Capercaillie; HG, Hazel grouse; PTA, Rock ptarmigan; PAR, Rock partridge. 'nh/na' refers to either to the fact that the species is not hunted ('no hunting') or that information is not available ('not available'). Sources and reference period: FR, Claude Novoa (comm.pers), 2012-2016 (approximate data); IT, this study, 2010-2015; CH, www.uzh.ch, 2011-2016; AUT, Stastistik Austria 2017, 2015-2017.*

	FR	IT	CH	AUT	DE	SLO
BG	**400**	**1141**	**483**	**1502**	nh/na	nh/na
CAP	nh/na	nh/na	nh/na	**355**	nh/na	nh/na
HG	nh/na	nh/na	nh/na	**118**	nh/na	nh/na
PTA	**50**	**165**	**490**	nh/na	nh/na	nh/na
PAR	nh/na	**566**	nh/na	nh/na	nh/na	nh/na

Alpine Galliforms management in Italy

In Italy, only Black grouse, Rock ptarmigan and Rock partridge are game species among the 5 Alpine Galliforms, as both Capercaillie and Hazel grouse are protected since the early 1990s. Despite being listed in Annex I and II of the Birds Directive and the unfavourable conservation status, Peronace et al. 2012, see also Table A1) there is no national survey on Galliforms in Italy. Thus, hunting districts bird counts actually provide the longest and most widespread survey of game birds on the Italian Alps, but the application of censusing methods can markedly differ between hunting districts and provinces, since according to current regulations, hunting is mostly under regional and provincial authority. As stated before in a broader sense, also in the particular case of the Italian breeding populations of Alpine Galliform species there are no reliable estimates (BirdLife International 2004; Brichetti and Fracasso 2004; Peronace et al. 2012; BirdLife International 2015a). Indeed, known population sizes are outdated and mostly derive from extrapolations of local data to national scale (Brichetti and Fracasso 2004; Franzetti and Toso 2009). Short- and long-term population trends are based on expert knowledge and do not rely on field data (Nardelli et al. 2015). As a consequence of this situation, Italy is the only western European country that lacks an evaluation of Black grouse population trend both at short- and long-term (BirdLife International 2015b). In addition, Rock ptarmigan and Rock partridge trend estimates are considered of poor quality (BirdLife International 2015c, d). Similarly, Italy does not have a national archive of Galliforms bags (Franzetti and Toso 2009), because hunting records at best are collected at regional or provincial scale.

Mandatory counts were first introduced in 1992 with the above cited Law 157/92 on wildlife protection. For this reason, standard monitoring was uncommon before 1993, when the national law was enforced at the regional level. Depending on the region, Galliforms counts are run by hunters and/or by game wardens and are usually performed twice a year, using standard techniques applied in most countries. Spring pre-breeding census (April-May) aims at evaluating densities and winter survival by counting males displaying in leks for Black grouse (Léonard 1989; Baines and Hudson 1995; Hancock et al. 1999) or singing in their territories for Rock partridge and Rock ptarmigan from points or along transects, with (Bernard-Laurent and Laurent 1984; Bernard-Laurent 1994a; Nopp-Mayr and Zohmann 2007; Marty and Mossoll-Torres 2011) or without (Bossert 1977) the help of playback calls. Reproductive success is evaluated in post-breeding summer counts (August-

September) with pointing dogs that help locating broods (Zbinden 1987; Ellison et al. 1988; Léonard 1992; Novoa et al. 2008).

Yearly, a shooting plan that establishes bag limits is set for each hunting district and it is usually based on the estimated breeding success of each species, derived from counts. Bag limits vary between different administrations. The plan is set by the local hunting authority, but it can derive from proposals of the boards of hunting districts. Grouse and partridge hunting is popular in the Western and Central Alps (e.g. Piedmont and Lombardy), but it is a marginal hunting activity in Eastern Alps (Veneto, Friuli-Venezia Giulia).

Only a limited number of authorities issued guidelines establishing minimum requirements for planning counts in terms of period, extent of sampling areas, methods and criteria for setting up the hunting plan. Thus, count data can markedly differ across administrations or even among hunting districts within the same administration. Only a few hunting districts or local administrations have a georeferenced database for storing data, or use at least a GIS for sampling areas definition or data archival.

Aims

In this Introduction I outlined the context in which the PhD project found its bases. The aim of the thesis has been the assessment of the vulnerability of Black grouse, Rock ptarmigan and Rock partridge Italian populations, focusing on abundance trends and conservation threats. More specifically, I performed i) a first-ever assessment of population trends of Alpine Galliform game species at national (Chapter 1 and Chapter 2) and regional/local level (Chapter 2), taking advantage of different available datasets, ii) an analysis of the effects of a major aspect of global change, that is land cover/land use changes, on Black grouse populations (Chapter 3) and iii) an evaluation of a possible adaptation of Rock ptarmigan marginal populations to sub-optimal climatic conditions through plasticity (Chapter 4). Hereafter I describe more in depth the specific goals and approaches, based on the context outlined in this introduction chapter.

Assessing vulnerability: population trends

The assessment of large scale population trends is part of the evaluation of species conservation statuses, and therefore has great relevance for the implementation of national and international environmental policies. Even if Alpine Galliforms are listed both in Annex I and Annex II of the Birds Directive and despite retaining a large portion of the Alpine territory, research on the conservation status of Alpine Galliforms in Italy is scarce if compared to other Alpine areas, such as France or Switzerland. In the former, a long term standardised survey is being organised by the Observatoire des Galliforms des Montagne (OGM) in collaboration with the Office National pour la Chasse et la Faune Sauvage (ONCFS, the state agency for wildlife and hunting management) and join research centres (CEFE - Montpellier). In Switzerland, there is a network of private and public institutions (Schweizerische Vogelwarte, WSL - Federal Institute for Forest, Snow and Landscape Research) and Universities (Bern, Lausanne) which research on population trends and environmental determinants. Hence, information on the conservation status of Alpine Galliforms populations is incomplete and unbalanced with the contribution of knowledge on Italian populations.

In this sense, the lack of a national survey scheme in Italy represents a further a threat to the conservation of these species, as potential large scale population declines are hardly detected from the sparse and not standardised available data, preventing the implementation of effective conservation measures.

Through this project, I aimed at filling this knowledge gap by estimating medium-term population trends of Black grouse, Rock ptarmigan and Rock partridge. This was accomplished by gathering scattered data on population abundances of the three game species and by estimating the bias in the current monitoring system enforced to local authorities and/or hunting districts. Two different population abundance proxies were employed for this purpose, that is, post-breeding counts and game bags, since they resulted being available at the widest spatial scale. The choice of using multiple proxies derives from the need to take advantage of all available information both in terms on data quantity (to improve precision and to extend the time frame of trend estimates) and data quality (as each proxy has its specific sources of bias).

I first started from comparing trends estimated from post-breeding counts and game bags using a classical approach implemented in TRIM software (Pannekoek and van Strien 2001), already in use in many bird monitoring schemes (e.g. PECBMS 2009; Géhin and Montadert 2016; Helle et al. 2016)

(Chapter 1), focusing also on different sources of bias such as hunting pressure, hunting effort and game management policies

Subsequently I worked on the development of a novel model which integrates both proxies, using state-space models (Kéry and Schaub 2012) (Chapter 2). This modelling approach was selected to limit the large expected observation error in the datasets, deriving from the abovementioned poor standardization of count methods and bias introduced by game management policies, Then, through the joint analysis of two datasets insisting on the same population, for which a common growth rate is assumed, I aimed at improving precision of the trend estimates by increasing data quantity, and possibly, at reducing bias.

Assessing vulnerability: land abandonment threatening Black grouse conservation in Italy

Land abandonment is considered a major driving force of global change in the Alps and it is remarkably evident in the Italian Alpine slope (Piussi and Pettenella 2000; Corti 2004; Motta et al. 2006; Falcucci et al. 2006; Tasser et al. 2007; Monteiro et al. 2011; Regione Lombardia and ERSAF 2012). After estimating population abundance changes in time, I focused on this specific threat to Alpine Galliforms conservation, which is somehow overlooked in research trends despite being an important environmental determinant (Anthelme et al. 2001; Maggini et al. 2014; Braunisch et al. 2016). This is especially true in Italy, where very few studies have been performed so far on this topic (Meriggi et al. 1998; Rotelli 2014; Ferrarini et al. 2017). Being an ecotonal species, Black grouse represents an ideal candidate to examine in depth the effect of shrub encroachement and densification of vegetation, and it is the only species for which in Italy georeferenced presence data date back to the early 1980s. In particular, I aimed at locating and quantify changes to the species potential distribution related to land cover changes only in Lombardy region (western-central Alps) that have occurred in a 30-year interval. More specifically, I developed a species distribution model (SDM) with a maximum entropy approach implemented with land cover belonging to 1980s and then predicted to present time using actual land cover. A specific goal was the detection of a differential change between inner and outer Alps related to the different timing of land abandonment in the two areas.

Assessing vulnerability: ecological plasticity of marginal populations

The degree to which environmental changes influence species conservation can buffered by either adaptive evolution or by phenotypic plasticity (Miner et al. 2005; Merilä and Hendry 2014; Valladares et al. 2014). While adaptation implies the selection of certain genotypes, phenotypic plasticity is defined as the capacity of a single genotype to exhibit variable phenotypes in different environments (Stearns 1989; DeWitt and Scheiner 2004; Nussey et al. 2005; Whitman and Agrawal 2009). Nevertheless, the disentaglement of genetic from environmental responses is not straightforward and often the two concepts are misused (Gienapp et al. 2008).

The evolutionary response of populations are likely to be inadequate to counter the speed and magnitude of climate change (Hoffmann and Sgrò 2011), even if microevolution can occur at fast rate (Reznick and Ghalambor 2001; Carroll 2008; Visser 2008). Therefore, plasticity is considered to play a important role in mitigating the effects induced by a warming and less predictable environment (Gienapp et al. 2008), at least at short- or medium term (DeWitt and Scheiner 2004).

Categories which were shown to exhibit some kind of plasticity in face of climate change in birds include morphology (e.g. body mass, Charmantier et al. 2008), phenology (Visser and Both 2005) and, most notably, distribution (Sekercioglu et al. 2008; Chen et al. 2011; Barbet-Massin et al. 2012; Elmhagen et al. 2015) and life-history traits related to the timing of breeding (display onset, laying date, hatching date), which have been observed advancing as a response of earlier onset of spring in many studies (Pearce-Higgins et al. 2005; Møller et al. 2006; Charmantier et al. 2008; Both and Visser 2011).

In the specific case of Alpine Rock ptarmigan, mixed responses to climate change have been shown, in terms of distribution shifts and timing of breeding from field data (Pernollet et al. 2015; Novoa et al. 2016). However, very few studies have directly addressed this topic by measuring in time some phenotypical trait, partly due difficulties with carrying on field research in such harsh environment. Hence, most of the species responses have been only predicted by models (Revermann et al. 2012; Imperio et al. 2013; Ferrarini et al. 2017), and there is a general lack of evidence of its capacity to counter the warming climate through plasticity.

Plasticity would be particularly relevant in marginal populations, which are more subject to experience the harshest climate warming. In case of the Rock ptarmigan, I refer to both biogeographical (distribution) and ecological (habitat) marginality. Being the species constrained by climate and, thus, by elevation, the two aspects often coincide, with geographical marginal or isolated populations living in sub-optimal environments at lower elevations. This marginality is a dynamic state resulting from the ongoing process of distribution/elevation shifts (Revermann et al. 2012; Pernollet et al. 2015). This determines the existence of a leading edge, where distribution is advancing, and a trailing edge, where distribution is shrinking (Hampe and Petit 2005). Given limited latitudinal and elevational dispersal possibilities of the species, marginality of trailing edge populations will increase under the pressure of climate change and would cause an increased extinction risk. In this scenario, individuals may be forced to exhibit some degree of plasticity to survive. This would result in an overestimated vulnerability of the species with respect to models predictions, that unanimously forecast a sharp decline of suitable habitat within the 21° century (Maggini et al. 2011; Revermann et al. 2012; Maggini et al. 2014; Ferrarini et al. 2017).

To test this hypothesis, I focused to a more general idea of "ecological plasticity", which refers to the capability of exhibiting flexibility in the face of change (Greenberg 1990), by comparing the use of habitat of two different Rock ptarmigan populations, one living on the trailing edge in a sub-optimal environment and another one living in an optimal environment in the core of the Alpine distribution. The goal was to evaluate whether the use of habitat of marginal populations could be more flexible with respect to core populations and, hence, to detect a plastic behaviour which would reduce the species vulnerability. In particular, in this preliminary study I analysed a small dataset of GPS locations, comparing the selection for topographical features of the two target populations.

Chapter 1

Where's the pulse to have the finger on? A retrospective analysis of two decades of Alpine Galliforms (Aves: Galliformes) census and game bag data in Italy

ABSTRACT. Information on the abundance of the Italian populations of Black grouse (*Lyrurus tetrix*), Alpine rock ptarmigan (*Lagopus muta helvetica*) and Alpine rock partridge (*Alectoris graeca saxatilis*) relies only on extrapolations of local data to the national scale, since there is no national standardized survey. Consequently, their status is virtually unknown. In this first Chapter, we performed a first-ever assessment of a medium-term (1996-2014) population trend of these species using and comparing post-breeding count and bag data at hunting district scale. These data were collected from various authorities in charge of wildlife management, and allowed us to test the influence of hunting policies on the estimated trends. Rock partridge showed a stable trend with numbers fluctuating between years, while there was evidence of a severe decline for the Rock ptarmigan. No general conclusion could be drawn for the Black grouse, as we detected lack of consistency of count and bag data. Counts were greatly overdispersed as a result of an uneven count effort among hunting districts. Adding the game management authority as model covariate resulted in more robust trend estimations, suggesting a significant effect of different policies, that emerged also as similar hunting pressure across species within authorities. Hunting effort variation over the time was instead negligible. Species-specific game management bias is discussed. Our results highlight the need for a survey scheme or guidelines to be applied uniformly at national scale.

KEYWORDS: Alps, grouse, status, Italy, hunting bags, game management

1.1 Introduction

The assessment of a species conservation status in a given area requires a reliable estimate of its abundance in time (Silveira et al. 2003; Kozlowski 2008; Newton 2013). This is usually achieved through the application of a standardised direct or indirect count method, repeated over the years (see Bibby et al. 2000; Sutherland 2006) or the collection of other abundance indices, such as road kills (Gehrt et al. 2002; Seiler et al. 2004; George et al. 2011; González-Gallina et al. 2016) and game bags (Chanin and Jefferies 1978; Moleón et al. 2008; Liberg et al. 2010; Rödel and Dekker 2012). At local scale, the assessment can be accomplished with good reliability, since it depends on a limited number of people and is usually tailored on the area and on the eco-ethology of the target population (Greenwood and Robinson 2006). At larger scales, such as regional or national, abundance assessment requires good supervision and coordination and is increasingly biased by differential skills and knowledge of the people involved, by possible under- or oversampling of areas and by the method that may not fit evenly (Sauer et al. 1994; Schmidt 2004; Reidy et al. 2011).

Monitoring of grouse populations has a long tradition in many parts of Europe and North America (Rogers 1963; Gates et al. 1968; Rajala 1974). Indeed, many grouse species are popular game birds and populations are locally surveyed in order to provide the basis for sustainable harvesting (Ellison et al. 1988; Aebischer 1991; Aanes et al. 2002). Anyway, local survey outcomes are often unsuitable when dealing with conservation issues at a large scale.

Although census methods are rather standardised (see Introduction), the actual implementation of such methods can broadly change between and within states, as a consequence of different game management principles and policies (see for a European review Putman et al. 2011), centralized or decentralized hunting authority, environmental characteristics (chiefly topography, Marty and Mossoll-Torres 2011), bird population densities (Höglund and Stohr 1997) and hunting traditions. Variability lies in the number, size and density of sampling areas, timing of counts, number of repeats per season, fieldworkers skill, use of playback devices and data recorded (sex, age etc.). Only a few countries have a common standardised monitoring scheme that leads to comparable estimates of population sizes and trends (e.g. Hudson 1992; Lindén et al. 1996) and supranational monitoring schemes are yet uncommon (Lehikoinen et al. 2014).

Hunting records represented historically the first proxy data for population trend assessment for game or harvested species, since Elton and Nicholson's pioneering work on Canadian lynx pelt-sale records (1942), and are still used to analyse long-term grouse population dynamics and trends (Barnes 1987; Cattadori et al. 2003a; Aebischer and Baines 2008; Ranta et al. 2008). In a few countries bag records proved to complete well or even substitute census data (Liberg et al. 2010; Soininen et al. 2016). Bag records reliability is questioned however, as variation in hunting effort can introduce significant bias (Ranta et al. 2008; Imperio et al. 2010; Willebrand et al. 2011) and therefore trends need to be corrected in order to provide meaningful results. However, if shooting plans are not used as means of providing sustainable harvesting, hunting effort can be easily accounted with the number of hunters or licenses issued per year (Imperio et al. 2010; Soininen et al. 2016), information which can be obtained by privately-owned hunting reserves or centralised public hunting authorities. Further bias may derive from weather conditions, which may limit hunters in case of persistent unsuitable weather, or from stocks dropping below critical densities, at which hunters' search is no longer fruitful and so they usually stop (Newton 2013).

As described in the introduction, Italy currently lacks a robust estimation on population trends of its Alpine Galliforms populations, since no national survey scheme is enforced and data is scattered among game management authorities.

In this study, we assessed the status in Italy of Black grouse (hereinafter BG), Alpine rock ptarmigan (PTA) and Alpine rock partridge (PAR), using count and bag data. We further tested i) whether count and bag data reflect similar trends, ii) the influence of game management policies and iii) whether hunting effort significantly changed over the studied period.

1.2 Materials and methods

1.2.1. Study area

According to the Italian legislation on wildlife protection (L. 157/92) that also regulates hunting, the Alpine territory is divided into hunting districts that manage hunting activities under provincial or regional supervision and control, since wildlife in Italy is state-owned and hunting is managed through a license system. Law 157/92 defines the Alpine territory as "the area where Alpine fauna lives" and it is shared between 5 regions (Valle d'Aosta, Piedmont, Lombardy, Veneto and Friuli-Venezia Giulia) and 2 Autonomous Provinces (Trento and Bolzano/Bozen). The game management districts extent is uneven among regions, mostly for historical reasons: the eastern Regions (Veneto, Trento, Bolzano and Friuli-Venezia Giulia) still adhere to a hunting regulation form originated under the Austo-hungarian Empire dominion in the XIX century, where hunting was regulated at the municipality level, and therefore hunting districts in Eastern Alps are almost municipality-sized (about 37 km^2, ISTAT 2013), whereas in the western Regions hunting districts are at sub-provincial size (in the order of magnitude of about 500 km^2). For the purpose of our study we grouped hunting districts data (counts and bags) of the eastern regions, in order to have an even dataset in terms of values range per surface area; if present (Trento, Friuli-Venezia Giulia), we used other game management entities that already group hunting districts. In the case of Belluno province of Veneto Region, we grouped hunting districts data to geographical coherent areas that matched the average size of the other districts. For this reason hereinafter we are using a more general "game manegement unit" (GMU) concept to identify the target areas. Overall, 72 GMU have been analysed, with an average extent of 468 (± 285) km^2 (**Figure 1.1**). Similarly, we associated each GMU to an "authority" representing the province or the region according to the administrative level in charge of game management, in order to evaluate the effect of different policies.

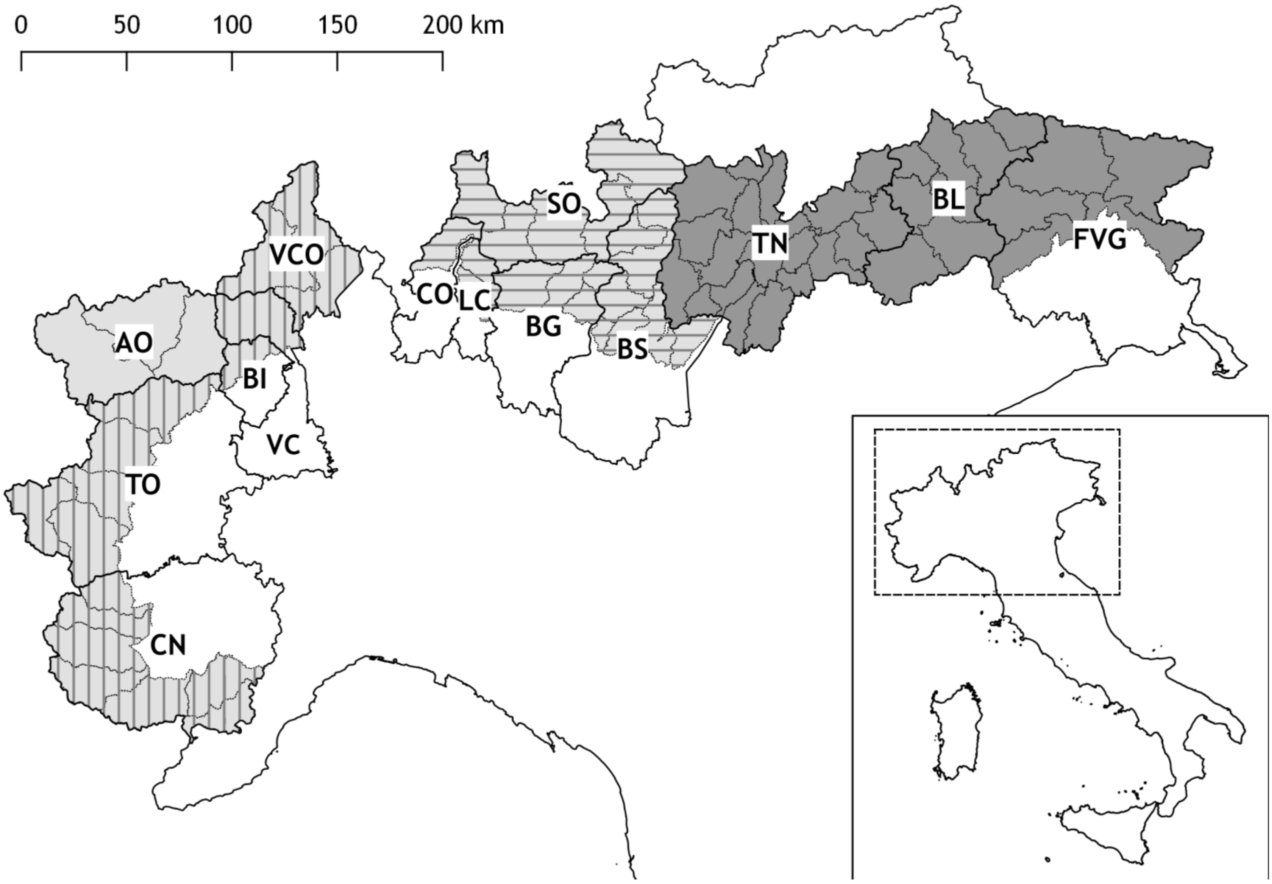


Figure 1.1 - *Location of the 72 Game Management Units (GMU) whose data have been analysed. Eastern regions, whose hunting district data were grouped due to different zoning, are shown in dark grey. Solid outlines represent game management authorities. Regions that do not correspond to authorities in our study are shown with filling lines (horizontal=Lombardy; vertical=Piedmont). CN=Cuneo, TO=Turin, AO=Aosta, BI=Biella, VC=Vercelli, VCO, Verbano-Cusio-Ossola; CO=Como, LC=Lecco, SO=Sondrio, BG=Bergamo, BS=Brescia, TN=Trento, BL=Belluno, FVG=Friuli-Venezia Giulia. Inset: location of the study area with respect to Italy.*

1.2.2. Count and bag data

Overall, counts, bag sizes and shooting plans were available as GMUs annual grand totals. Data were collected from 72 GMUs, covering the whole Italan Alps with the exception of Bolzano/Bozen Autonomous Province. Game bags and bird counts were used to calculate population trends, while shooting plan data were used as a proxy variable to evaluate hunting effort. Post-breeding counts were chosen as state variable since only few districts regularly perform pre-breeding counts, which are more commonly used to estimate population trends. Data series lengths are uneven by species and variables, as well as by GMU (**Table S1.1**), due to different archival policies and harvest suspensions or bannings. Further details on data characteristics are found in the Introduction.

1.2.3. *Data analysis*

1.2.3.1. Trend analysis.

Population trends of the target species were estimated using TRIM (Pannekoek and van Strien 2001), a software used in many bird monitoring schemes (e.g. PECBMS 2009; Géhin and Montadert 2016; Helle et al. 2016) and for each species two separate trend estimations were carried out using game bags and post-breeding counts data series. Due to unequal time series length, we limited our dataset from 1996 to 2014. Considering the three studied species and the two putative state variables, we calculated 18 trend estimates using TRIM as follows: a first model (linear model) was calculated with a linear trend function and default options, without accounting for covariates and assuming a random effect of time. In a subsequent TRIM run, we added data origin (i.e. authority) as a covariate (covariate model) to test for game management fixed effect. A final run used a refined model considering a fixed effect of time, i.e. checking for significant nonlinearities in trends (nonlinear model). We were unable in the latter case to use data origin as a covariate due to missing data for some authorities. Spatial variation of trends can depend also on environmental factors, such as climate and habitat, acting at larger scale, but grouping authorities at regional level resulted in weaker models or non-significant regional covariate (for details see Table S1.3). Trends are calculated on the estimated log-transformed annual population totals. For all three models, TRIM was configured to account for serial correlation and overdispersion and to use 2001 index as base index (2001 index = 1.00). Model robustness was evaluated through comparison of AIC and overdispersion values provided by the software. An autocorrelation test was performed on bag and count indices to check for population cycles, using *Acf* function in forecast R package (Hyndman and Khandakar 2008).

1.2.3.2. Proxy comparison.

We tested the consistency of bags and counts building for each species a linear regression model with count and bag TRIM indices as dependent variable, year as continuous independent variable and proxy type (bag or count) as categorical independent variable, adding the year by proxy type interaction to assess for significant differences in slopes. For each species and proxy we used indices from the models with lowest AIC values. Bag values of Trento province were removed from this analysis since for this authority count data were unavailable. Since the regressions were performed on time series data, we used a GLS (Generalized Least Squares) method to account for auto-correlation structure of residuals. We further tested whether counts and bags were correlated by performing a pairwise Pearson's correlation on indices series that was previously differenced to meet the assumptions of independence and stationarity by removing autocorrelation and trends. Data analyses were performed using R software, version 3.3.2, *gls*, *cor* and diff functions from *nlme* and *base* packages (Pinheiro et al. 2016; R Core Team 2017).

1.2.3.3. Hunting effort.

The utilization of bag data as proxy for population abundance requires the evaluation of hunting effort, which is usually calculated as the number of hunters or hunting licenses issued per year (e.g. Imperio et al. 2010; Soininen et al. 2016). In Italy the number of hunters has decreased in the last decades (ISTAT 2013), but these information is not available at local scale, so we were unable to relate bag data to number of hunters or hunting days. The policy of shooting plans adopted in Italy can partly overcome the bias introduced by the variation of the number of hunters over time, since the annual yield in each district is limited at the top regardless of the hunting effort, but it may not control if hunting effort decreases, which is the most likely scenario. Assuming that shooting plans were proportional to summer counts (i.e. population abundance), we used annual yield/shooting plan ratio in each GMU as proxy for hunting effort. The ratio can occasionally exceed 1 if early closure of the hunting season is delayed despite the shooting plan is about to be completed. We assessed linear trends in hunting effort by regressing the ratio against years for each GMU and then we calculated the mean of the slopes of all significant ($p<0.05$) regressions. Autocorrelation of the error at lag 1 was tested with a Durbin-Watson test for autocorrelation of disturbances, using *dwtest* function in *lmtest* R package (Zeileis and Hothorn 2002). Hunting units showing significant autocorrelation were modelled with a GLS (Generalized Least Square) linear regression method. Since in some GMUs hunting had been opened only for few years, regression was applied only to time series spanning for at least 10 years. Hunting effort on BG in Valle d'Aosta region was assessed at regional level because according to the local hunting regulations the plan is set for the whole region and not subdivided among hunting districts. Regressions were performed using R software, version 3.3.2, *lm* and *gls* functions from *stats* and *nlme* packages (Pinheiro et al. 2016; R Core Team 2017)

1.2.3.4. Hunting pressure.

Hunting pressure is one of the main features of game management. In Italy, hunting pressure is regulated by setting of shooting plans, but since criteria to set plans are at best established at regional scale, we tested for hunting pressure differences across management authorities. Within authorities, we also compared hunting pressure across species in order to show possible common patterns. We elaborated a hunting pressure index (HPI) based on the catch-per-unit-area (CPUA) of species' suitable habitat. For each species and GMU, we estimated the extent of suitable habitat by reclassifying the Corine Land Cover map (Büttner et al. 2014) according to species' ecology. Then, we calculated the log-transformed ratio of the annual bag values and the estimated size of suitable habitat. An annual HPI for each species and GMU was defined as the difference between bags/habitat ratio and the species' GMU median value. A MANOVA with Wilks' statistic was performed to test for common effect of the hunting authority on the three species using *manova* function from *stats* R package (R Core Team 2017), after testing the assumption of normal distribution of residuals with Shapiro-Wilk's test. The MANOVA was run using only full combinations of annual HPI for the three species (n=345). Univariate ANOVA was also performed to check for the effect of authority on single species.

1.3 Results

1.3.1. Trend analysis and proxy comparison

The proportion of missing values imputed by TRIM for both game bags and count data ranged from 11.5% to 36.1% depending on the species and proxy variable, with the lowest proportion in BG bag data and highest in PAR bag data (**Table 1.1**).

Considering the period 1996-2014, all game bag-based models estimated a negative trend for the three species, while only PTA showed significant negative trend according to count data (**Table 1.1**). Bags estimated for BG a mean annual population reduction equal to 2.1-2.4% depending on the model, whereas according to counts BG populations remained essentially stable (-0.5 / +0.1%; Wald test on significance of slope in the linear model, p=0.449).

Both bags and counts showed a negative trend for PTA (-3.9/-5.4%). PAR populations are characterized by fluctuations over the considered time span both in bag- and count-based models that ultimately resulted in a negligible negative trend according to bags (-0.9/-1.2%), while counts estimated a stable trend (-0.4/+0.2%; Wald test on slope parameter, p=0.14). A major feature that emerged was a population peak in 2006-2007 and two troughs in 2001 and 2011, resulting both in bags- and count-based models. A significant negative autocorrelation was found at lag 6 (-0.607, CI 95% ±0.449) in bags time effect model and at lag 5 and 6 (-0.527 and -0.518, CI 95% ±0.449) in counts time effect model. Conversely, no significant autocorrelation was found in BG and PTA.

In bag-based models, the lowest AIC values were provided by the time effect models for all species. Conversely, covariate models were selected in BG and PTA count-based models, while still the time effect model performed better in PAR counts. Nevertheless, covariate models performed better than the linear models and the effect of the authority covariate is highly significant (Wald test, p<0.01) for all species and proxy variable. Count data were highly overdispersed relative to bags, with overdispersion values far beyond the suggested threshold for TRIM use (Pannekoek and van Strien 2001). Bag-based models exceed the 3.0 threshold only for PAR, while count-based models overdispersion values was up to 6-fold.

Bags and counts slopes were significantly different as evidenced by the GLS regression interaction term for BG (0.017, p=0.018), but not for PAR and PTA (respectively, p=0.515 and p=0.906). Conversely, pairwise Pearson's correlation on differenced indices emerged for PAR (r=0.77, p<0.001), but not for BG and PTA (respectively, BG, r=-0.05, p=0.839; PTA, r=0.03, p=0.890). We concluded that slope consistency between bag- and count-based PTA models may be spurious, since a significant correlation would be expected if the two variables described annual abundance likewise. Albeit GLS regression accounts for autocorrelation, it must be noted however that fitting a linear model through the peaks and troughs of PAR population resulted in high standard errors. This constrained the power of the model and the capability to detect different trends between proxies.

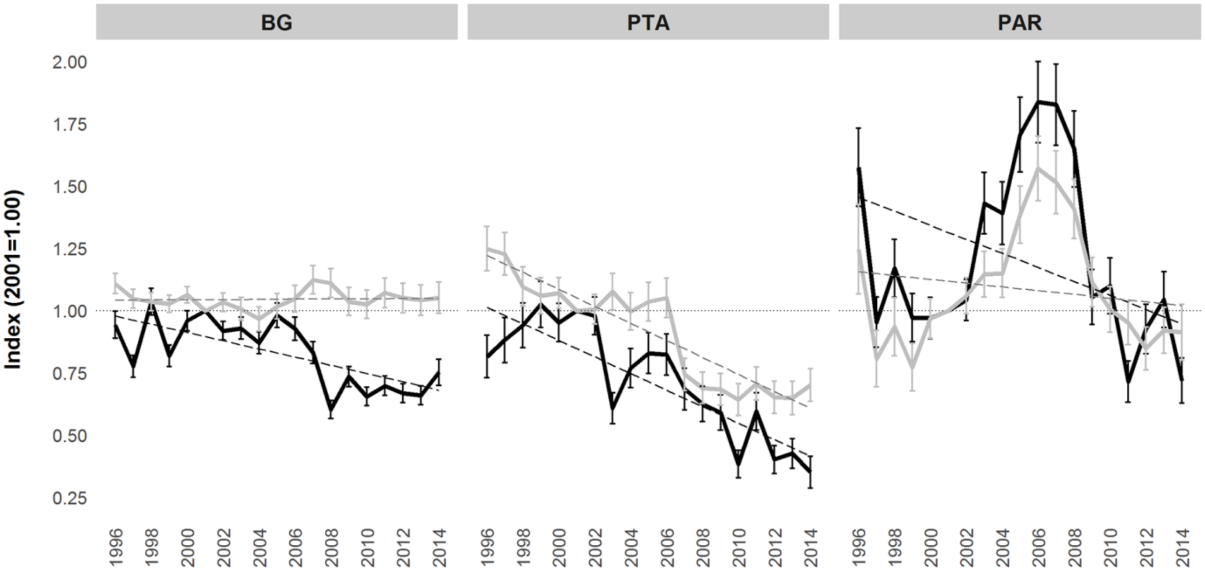


Figure 1.2 *Population indices of the three target species (BG=Black grouse; PTA=Rock ptarmigan; PAR=Rock partridge), selected from the models with the lowest AIC values (BG and PTA counts = covariate; the remainders = time effect). Gray solid lines represent count indices, black solid lines represents bag indices. GLS regressions fitted through population indices are shown with dashed lines*

Table 1.1 - *Model comparison and additive annual growth rates (on log transformed annual population indices) as calculated by TRIM software. Wald test values refer alternatively to significance of slope parameter (linear model), authority covariate (covariate model) and deviations from linearity (time effect model). Significance in terms of p-value are indicated by asterisks (*, ≤ 0.05; **, ≤ 0.01; ***, ≤ 0.001). Overdispersion is calculated with respect to a Poisson data distribution.*

Species	proxy	n sites	n obs.	% missing	model	overdisp.	AIC	Wald test		trend
BG	**Bags**	72	1368	11.5	linear	2.598	897.0	73.7	***	-0.023
					covariate	2.339	595.2	80.6	***	-0.024
					time effect	2.385	499.9	152.5	***	-0.021
	Counts	52	988	31.7	linear	17.327	9523.9	0.6		-0.002
					covariate	15.868	8579.6	38.3	***	0.001
					time effect	16.945	9571.5	28.4	*	-0.005
PAR	**Bags**	60	1140	36.1	linear	4.283	1867.7	6.2	*	-0.009
					covariate	3.901	1568.5	34.4	***	-0.012
					time effect	2.964	631.8	244.2	***	-0.012
	Counts	50	950	32.0	linear	22.102	15396.5	0.4		-0.004
					covariate	20.189	13707.5	34.6	***	0.002
					time effect	16.764	9215.8	109.5	***	0.002
PTA	**Bags**	39	741	35.4	linear	2.230	287.0	71.4	***	-0.049
					covariate	2.095	204.9	24.9	**	-0.050
					time effect	1.996	44.1	71.8	***	-0.053
	Counts	30	570	35.1	linear	10.044	3604.3	71.9	***	-0.054
					covariate	7.315	2253.3	80.3	***	-0.039
					time effect	10.103	3466.0	30.3	*	-0.051

1.3.2. Hunting effort

We detected a limited variation in time of the bag/plan ratio for all three species. Regression slope coefficients for BG, PAR and PTA were significant ($p<0.05$), respectively, in 19% ($n=69$), 28% ($n=44$) and 8.5% ($n=35$) of the GMUs. In addition, mean significant coefficients were small (BG, 0.007 ± 0.020, $n=8$; PAR, 0.027 ± 0.026, $n=12$; PTA, -0.009 ± 0.039, $n=3$), indicating that hunting effort variation could be considered negligible on the estimated bag-based trends. Nevertheless, positive average slope values emerged for BG and PAR are not consistent with the hypothesis that hunting pressure would have likely decreased in time following the downward trend of number of hunters.

1.3.3. *Hunting pressure*

MANOVA performed on the HPI was highly significant ($F_{8,336}$ =19.314, p<0.001, Wilks' lambda = 0.322), evidencing that the hunting pressure is a distinctive feature of the authority regardless of the species. Only a limited number of combinations year*GMU*species were available for the MANOVA, since hunting to all three species during the considered period occurred only in some GMUs. Nevertheless, similar hunting pressure emerges also in authorities that allow only BG and PAR hunting, as shown in **Figure 1.3**. Authorities with highest hunting pressure are all located in Lombardy region, which is the only one that lacks management guidelines (see **Table S1.2**). Conversely, low hunting pressure is present in regions that defined guidelines on shooting plans or with a regional management authority that acts as a control on hunting.

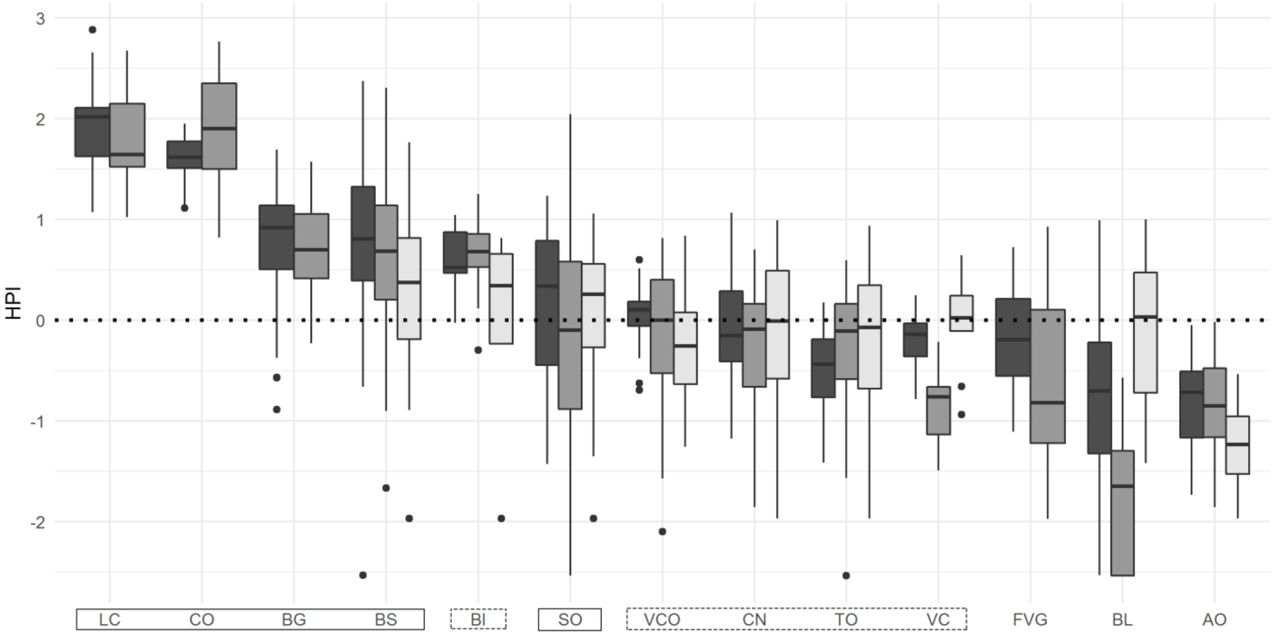


Figure 1.3 *- Comparison of hunting pressure across authorities and species (dark gray=BG; intermediate gray=PAR; light gray=PTA). HPI (hunting pressure index) is calculated as log-transformed ratio of annual bag size of each GMU and estimated extent of suitable habitat for each species and GMU, minus the species' median value. The plot is sorted by authorities' median values. Highest values are found in Lombardy (solid outline) and Piedmont (dashed outlines) regions.*

1.4 Discussion

Choosing the best proxy data is crucial in the evaluation of the status of a species (Joseph et al. 2006), especially in poor data systems (Popescu et al. 2016). Data on the Italian populations of BG, PTA and PAR fit this definition, as already highlighted by the latest national reports on the application of the Birds Directive (Nardelli et al. 2015) and on conservation status of game species (Franzetti and Toso 2009). Our study addressed this issue by performing a medium-term evaluation of population trends of these species considering two different data sources and evaluating the effect of hunting policies on data.

In managed wildlife populations, both counts and bags statistics are influenced by game management policies (see Apollonio et al. 2010). Galliforms hunting in the Italian Alps makes no exception from the results of our study, as we detected a significant effect of the game management authority on both count and bag data in all species. Extrapolations of local data to national scale as a tool to assess the species' conservation status is therefore misleading if data authority source is not accounted. Covariate count-based models were selected over time effect models for BG and PTA. For these species, accounting for game management by means of a fixed effect of the authority resulted in more robust models then accounting for a fixed effect of time. Conversely, for bag-based models, time effect models were selected over covariate models for all species, suggesting that game management may have less influence. Overdispersion of counts is remarkably high and cannot be explained only by means of different population densities, since all species are evenly distributed across the Italian Alps, especially BG (Brichetti and Fracasso 2004). Thus, overdispersion of counts is likely to result from an uneven count effort among GMUs (e.g. number and size of sampled areas), which ultimately derives from different game managements. On the other hand, the decreasing number of hunters that is occurring at national scale seems not to plausibly affect the robustness of bags as state variable for population abundance.

However, jumping to the conclusion that bags should be chosen over counts to estimate trends of Italian Galliform populations could be misleading since species-specific considerations should be made. As a general rule, a strong relationship between post-breeding counts and game bags of subsequent hunting season is expected, even when shooting plans are set, since the breeding success evaluated through post-breeding counts is the parameter most commonly used to limit annual yields to a sustainable rate. From the results of our study, this seems to apply well only to PAR, while both BG and PTA show specific inconsistencies.

BG was characterized by a significant difference between the trends estimated by bags and counts, with a strong divergence in 2003-2008. In this period bags markedly declined even though counts remained stable. We speculate that this lack of consistency is likely to result from changes in game management policies that occurred during that period. In fact, some local administrations issued guidelines that established parameters to set shooting plans given the results of summer counts (i.e. Piedmont region and Trento Autonomous Province, both in 2004), therefore limiting subjectivity that used to lead to higher harvests. This hypothesis may explain why hunting effort seemingly increased in some GMUs. The underlying assumption that shooting plans are proportional to population abundance estimated through summer counts may not be effective throughout all the time span considered. Given the number of hunters (i.e. the true hunting effort), the bag/plan ratio may have increased as a consequence of a progressive reduction of shooting plans with respect to summer counts. In other terms, game management policies changed from less to more conservative, accordingly to an increased control on game management policies resulting from the Natura 2000 network and EU Birds Directive enforcement. This likely happened also to PAR, as we found an increase in the bag-to-plan ratio in 12 out of 44 analysed GMUs, despite the trend difference between bags and counts resulted not significant due to limited power of the model with highly autocorrelated errors.

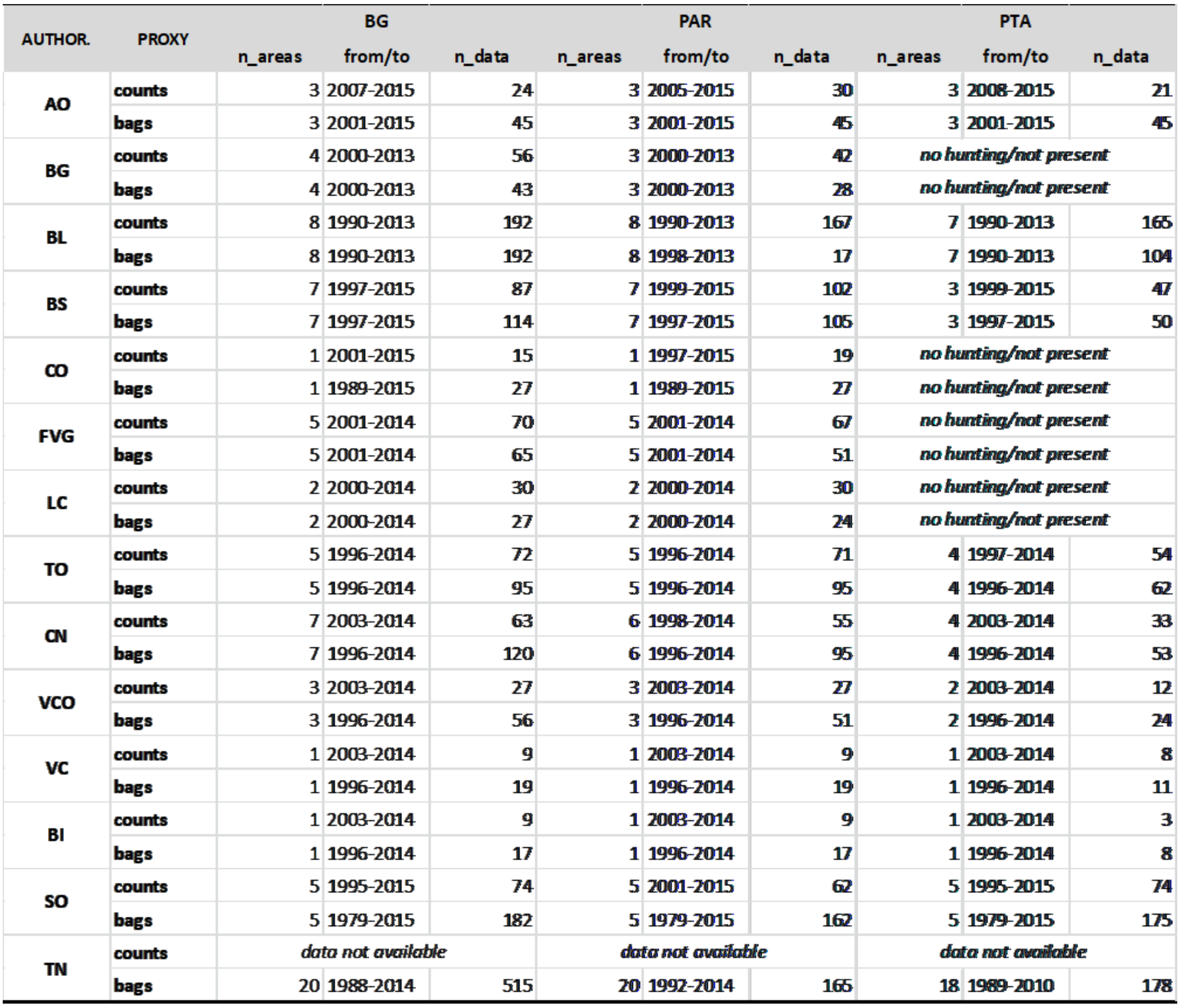
In the case of PTA, population TRIM model slopes of bags and counts series were similar and not statistically different as evidenced by the GLS regression, but the result emerging from the Pearson's correlation suggests that proxy consistency is spurious. Thus, population abundance reduction that occurred in the considered time span shaped the trends independently. This consideration has a great relevance from a management point of view, since it implies that the two proxy may be used either to assess the species' national status only in case of a persistent sharp trend, but minor changes or fluctuations might not be detected likewise. In other terms, population reduction likely represents the main driver of the observed PTA negative trend both for counts and bags, but other factors may affect the estimates. For example, PTA hunting is heavily affected by weather conditions occurring during the two-months hunting season. In fact, early snowfalls may limit access to hunting grounds causing a mismatch between count and bag data. This is the case of 2003, when persistent snow cover at the end of October was reported in many locations below 1800 m a.s.l (ARPA Lombardia 2003) and it was recorded in the bag series by a trough in the trend. For this trough there are no basis to speculate on a possible increased mortality in autumn caused by early snowfalls, since weather effects on population dynamics has been reported in many grouse species mostly in spring and summer (Scherini et al. 2003; Novoa et al. 2008; Furrer et al. 2016; García-González et al. 2016). Effects of game management on trends also emerged as a sharp decline in counts and, less evidently, in bag series in 2007. In this year the Italian government enacted a law (DM 17/10/2007) on minimum conservation criteria in Natura 2000 sites, that transposed the EU “Habitat” 92/43/EEC and “Birds” 2009/147/EC Directives. According to this law, PTA hunting in Natura 2000 sites was forbidden, resulting in a massive reduction of available area open to PTA hunting, given that the 60% of the Italian breeding population is estimated to be located within SPAs (Nardelli et al. 2015). As a result, many sample areas in hunting grounds ceased to be surveyed, since only the estimated breeding success in hunting grounds is used as reference data for setting the shooting plans.

Italian PAR population shows an overall stable trend in the considered period according both to counts and bag data and appears to be characterized by a major 10-year cycle as evidenced by the autocorrelation. Population cycles are typical of grouse species, mostly in Boreal regions (Ranta et al. 1995; Kvasnes et al. 2009; Lampila et al. 2011), but also PAR populations are known to exhibit cycles (Cattadori et al. 1999), despite the observed lag is larger than the 4-7 years lag reported. Larger lags may derive from a harmonic effect of multiple lags, as hypothesized by Cattadori et al. (1999). Interestingly, the same population peak has been recorded also in Swiss populations that is based on pre-breeding counts (Sattler et al. 2016). However, further analyses with longer series are needed to confirm cyclic behaviour of PAR populations, since our 19-year time series fits only one full cycle. Among the three target species, PAR is the only species with consistent count and bag trends. We speculate that this feature derives from peculiar characteristics of PAR hunting in Italy. Firstly, bags are hardly biased by weather conditions during the hunting season, as in PTA hunting, since PAR avoids slopes with persistent snow cover and it is then pushed to lower altitudes by snowfalls, where it is reached by hunters without difficulty. Secondly, PAR hunting is practiced by fewer hunters compared to BG hunting, which is the most popular species among *tipica alpina* hunters. This leads to a high quality standard of post-breeding counts, because they are often run by few skilled hunters and dogs over the years, with high knowledge of the eco-ethology of PAR and their hunting grounds, thus reducing the bias introduced by the observers.

Albeit managed by regulations, the role of hunting as threat to Galliforms conservation is debated (Aebischer 1991; Ellison 1991; Sandercock et al. 2011). We showed that hunting pressure is remarkably different on the Italian Alps. As already mentioned, this denotes that Galliform hunting is not evenly important within local traditions of western and eastern Alps, but highest pressures are found in absence of regional control on game management, such as Lombardy, in which management used to be entirely delegated to provincial scale until 2015. We are unable to evaluate whether higher pressures are locally affecting the species' conservation, since more robust data on spring abundance and breeding success are required. Nonetheless, this lack of common guidelines at larger scale leaves populations at the risk of overexploitation.

1.5 Appendix 1

Table S1.1 - *Data series length and number of data according to authorities, species and proxy.*



AUTHOR.	PROXY		BG			PAR			PTA	
		n_areas	from/to	n_data	n_areas	from/to	n_data	n_areas	from/to	n_data
AO	**counts**	3	2007-2015	24	3	2005-2015	30	3	2008-2015	21
	bags	3	2001-2015	45	3	2001-2015	45	3	2001-2015	45
BG	**counts**	4	2000-2013	56	3	2000-2013	42	*no hunting/not present*		
	bags	4	2000-2013	43	3	2000-2013	28	*no hunting/not present*		
BL	**counts**	8	1990-2013	192	8	1990-2013	167	7	1990-2013	165
	bags	8	1990-2013	192	8	1998-2013	17	7	1990-2013	104
BS	**counts**	7	1997-2015	87	7	1999-2015	102	3	1999-2015	47
	bags	7	1997-2015	114	7	1997-2015	105	3	1997-2015	50
CO	**counts**	1	2001-2015	15	1	1997-2015	19	*no hunting/not present*		
	bags	1	1989-2015	27	1	1989-2015	27	*no hunting/not present*		
FVG	**counts**	5	2001-2014	70	5	2001-2014	67	*no hunting/not present*		
	bags	5	2001-2014	65	5	2001-2014	51	*no hunting/not present*		
LC	**counts**	2	2000-2014	30	2	2000-2014	30	*no hunting/not present*		
	bags	2	2000-2014	27	2	2000-2014	24	*no hunting/not present*		
TO	**counts**	5	1996-2014	72	5	1996-2014	71	4	1997-2014	54
	bags	5	1996-2014	95	5	1996-2014	95	4	1996-2014	62
CN	**counts**	7	2003-2014	63	6	1998-2014	55	4	2003-2014	33
	bags	7	1996-2014	120	6	1996-2014	95	4	1996-2014	53
VCO	**counts**	3	2003-2014	27	3	2003-2014	27	2	2003-2014	12
	bags	3	1996-2014	56	3	1996-2014	51	2	1996-2014	24
VC	**counts**	1	2003-2014	9	1	2003-2014	9	1	2003-2014	8
	bags	1	1996-2014	19	1	1996-2014	19	1	1996-2014	11
BI	**counts**	1	2003-2014	9	1	2003-2014	9	1	2003-2014	3
	bags	1	1996-2014	17	1	1996-2014	17	1	1996-2014	8
SO	**counts**	5	1995-2015	74	5	2001-2015	62	5	1995-2015	74
	bags	5	1979-2015	182	5	1979-2015	162	5	1979-2015	175
TN	**counts**	*data not available*			*data not available*			*data not available*		
	bags	20	1988-2014	515	20	1992-2014	165	18	1989-2010	178

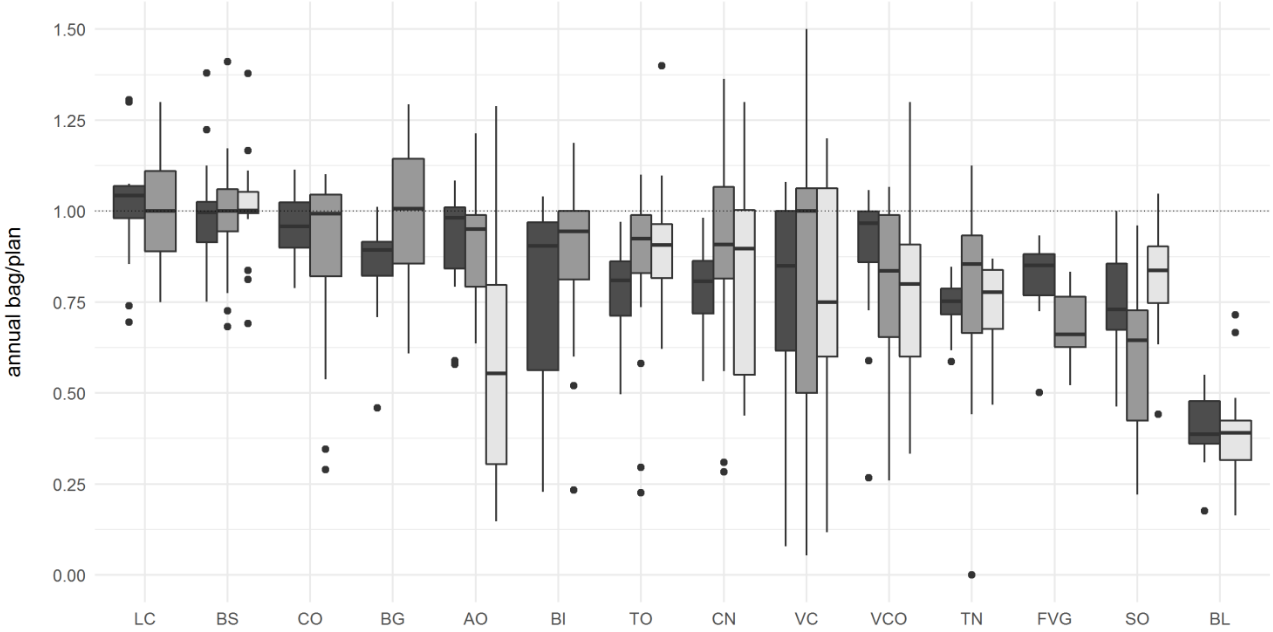


Figure S1.1 - *Comparison of hunting effort across authorities and species (dark gray=BG; intermediate gray=PAR; light gray=PTA). The plot is sorted by authorities' median values.*

Table S1.2 - *Game management regional characteristics. Hunting pressure is evaluated as average catch per unit of suitable habitat, calculated at provincial level (see Figure 1 for details). Counts guidelines specify whether the region issued guidelines for sampling areas definition, count timing and methods. Shooting plans guidelines refers to common criteria to set shooting plans. "Partial" hunting can be spatial (only in some areas) and/or temporal (recurrent suspensions or bannings). Notes: (1) the region consist of an only province; (2) the province is autonomous and has region-like powers; (3) we considered data of an only province, due to extremely small bag and count sizes of the remainder provinces; (4) only 2 out of 5 provinces issued guidelines*

	Hunting district size	Authority	Hunting pressure	Counts guidelines	Shooting pl. guidelines	BG hunting	PTA hunting	PAR hunting
PIEDMONT	Sub-prov	Province	average	yes	yes	yes	yes	yes
AOSTA VALLEY	Sub-prov	Region (1)	low	yes	yes	yes	yes	yes
LOMBARDY	Sub-prov	Province	high	no (4)	no (4)	yes	yes	yes
TRENTINO	Community	Province (2)	average	yes	no	yes	no	no
VENETO	Community	Province (3)	low	no	yes	partial	partial	partial
FVG	Community	Region	low	no	yes	partial	no	partial

Table S1.3 - *Comparison between TRIM covariate models (game management authority / region). Aosta Valley region was grouped with Piedmont in this analysis, due to potential bias introduced by the small size.*

Species	proxy	n sites	n obs.	% missing	covariate model	overdisp.	AIC	Wald test		trend
BG	Bags	72	1368	11.5	authority	2.339	595.2	80.6	***	-0.024
					region	2.411	701.3	46.5	***	-0.024
	Counts	52	988	31.7	authority	15.868	8579.6	38.3	***	0.001
					region	17.417	9509.6	2.8		-0.002
PAR	Bags	60	1140	36.1	authority	3.901	1568.5	34.4	***	-0.012
					region	4.05	1687.6	19.5	**	-0.011
	Counts	50	950	32	authority	20.189	13707.5	34.6	***	0.002
					region	21.971	15210.6	4.5		-0.002
PTA	Bags	39	741	35.4	authority	2.095	204.9	24.9	**	-0.050
					region	2.2	264.6	8.3		-0.050
	Counts	30	570	35.1	authority	7.315	2253.3	80.3	***	-0.039
					region	7.354	2336.2	73.5	***	-0.039

Chapter 2

An integrated state-space model to assess Italian Alpine Galliforms status from count and bag data

ABSTRACT. In Chapter 1 we performed a first-ever assessment of a medium-term trend of Italian Black grouse, Rock partridge and Rock ptarmigan Alpine populations, using separately population indices obtained from count and bag data. This has led to uncertainty in the estimates, as the two proxies were consistent only for Rock partridge. Using the same dataset, in Chapter 2 we elaborated an integrated state-space model that sources information from counts and bags jointly to estimate population growth rates at various spatial scales. In the model, we assumed *a priori* that year-to-year population changes at site level for both bags and counts reflected the same growth rate, that eventually became the link parameter allowing integration between datasets. The integration of counts and bags succeded in improving growth rate parameter precision and in reducing proxy-specific bias by increasing the sample size and extending data series length. With respect to the results of Chapter 1, the integrated model succeded in weighting the disproportionate effect of sites with count and bag values far exceeding the average, resulting in a different estimation of Rock partridge trend. On a 19-year basis, the national trends for the three species were consistent with the current conservation status reported in the Italian Red list of birds (LC for Black grouse, VU for Rock partridge and Rock ptarmigan). No evident regional patterns emerged, as a likely effect of a prevailing influence of local environmental conditions. Some potential applications of this model to other wildlife monitoring cases are reported.

KEYWORDS: Alps, grouse, status, Italy, integrated model, uncertainty

2.1 Introduction

The assessment of wildlife population sizes and their trends is one of the most important research fields in conservation biology (Shaffer 1981; Soulé 1991; Dobson 2005). Population surveys allow the monitoring of the conservation status of populations, the potential identification of declining trends and vulnerability and, eventually, promote the activation of management actions (Yoccoz et al. 2001; Nichols and Williams 2006).

This is usually achieved through field monitoring techniques and data modelling, but the results often deal with a certain amount of uncertainty deriving from several sources of noise. For example, census methods may not fit to the selected population/species, not be fully standardised in time and space or be differently implemented (Thomas 1996; Thompson 2002; Roberts and Schnell 2006); sampled subpopulations dynamics may not be representative of the whole target population (Brown et al. 1995; Guo et al. 2005); detectability of individuals could be uneven due to the heterogeneity of environmental conditions, weather conditions or accessibility to sampling areas (Watkins et al. 2010; Anderson et al. 2015); finally, data could be opportunistic or derive from indirect observational schemes (Sáenz–Arroyo et al. 2005; Cromsigt et al. 2009; McPherson and Myers 2009). Regardless of the nature of noise, this stochasticity in population surveys is grouped into a more general “observation error” in population modelling (de Valpine and Hastings 2002; Clark and Bjørnstad 2004).

Several methodological improvements to deal with observation errors have been developed in the assessment of population sizes in order to get reliable trends, both in field techniques (e.g. double observer counts, Nichols et al. 2000, Forcey et al. 2006; repeated surveys, Svensson 1979) and data modelling (e.g. N-mixture modelling for imperfect detection, Kéry et al. 2005). Minimising this uncertainty and getting robust and unbiased trend estimates is a crucial issue in conservation biology in order to trigger appropriate conservation measures if needed, and, in exploited populations, to set up a proper management considering sustainable harvesting goals. Misinterpretation of population growth rates with high degree of uncertainty may lead to management policies failures with detrimental consequences to conservation of the target populations (Nichols et al. 1995).

State-space models (SSM) represent a natural approach to deal with observation errors, as they allow the disentanglement of the real, unobserved demographic processes from the observation process of data collection within the observed change in population size (Kéry and Schaub 2012; Gimenez et al. 2012). SSM are very flexible and have been recently applied to a wide range of studies, such as movement ecology (Anderson-Sprecher and Ledolter 1991; Patterson et al. 2008), occupancy (Royle and Kéry 2007) and, chiefly, population dynamics, often involving CMR (Besbeas et al. 2002; Pradel 2005; Gimenez et al. 2007; King 2012). SSM have been largely applied also to the estimation of population trends (Chaloupka and Balazs 2007; Hefley et al. 2013; Davis et al. 2014; Furrer et al. 2016), which represents a synthetic index providing a quick tool to assess the species conservation status at large spatial scales.

Besides the need to reduce uncertainty, ecologists often have different elements of the analysed biological system scattered in several different datasets (i.e. survival from capture-recapture data, recruitment from surveys at breeding sites, immigration/emigration from telemetry data). Such diverse methods provide valuable information, but the joint inference is often made by analysing the datasets separately and comparing the output of population projections based on demographic parameters with the observed growth rates from count data (Coulson et al. 2001). This adds uncertainty in the analysis as not all demographic parameters are usually available and, thus, properly accounted in the projection. Integrated population modelling is a relatively novel approach that overcomes this issue by performing a joint likelihood from the likelihoods calculated from single datasets (White and Lubow 2002; Jenouvrier et al. 2003; Schaub et al. 2007; Zipkin and Saunders 2018). This feature allows the joint analysis of abundance data and demographic parameters efficiently (Besbeas et al. 2002, 2003; Freeman and Crick 2003; Schaub and Abadi 2011), and, possibly, to derive demographic parameters directly from the model without measuring them on the field (Tavecchia et al. 2009; Abadi et al. 2010b). It has yet been applied to many wildlife research areas, most notably, to threatened species, where information available is often limited and therefore it is advisable to take advantage of all available information (Freeman and Crick 2003; Schaub et al. 2007; Véran and Lebreton 2008; Rhodes et al. 2011) and to fishery and game species (Meyer and Millar 1999; White and Lubow 2002; Chee and Wintle 2010; Maunder and Punt 2013; Davis et al. 2014).

In game species, the estimation of population abundance is usually based on two kind of proxies, i.e. counts in sample areas and analysis of game bags (Rogers 1963; Cattadori et al. 2003a; Ferreira et al. 2010). Game bags records have been widely used as means to get population trends since they are usually collected at large spatial scales and longer temporal span than counts (Cattadori et al. 2003a; Aebischer and Baines 2008; Imperio et al. 2010; Elmhagen et al. 2011; Ueno et al. 2014). Hence, some of the longer-lasting population surveys rely on bag information (Mysterud et al. 2002; Aebischer and Baines 2008) as well as national population indices (Moleón et al. 2013). Moreover, in resource-limited contexts, hunting statistics provide a feasible monitoring system compared to more elaborated count schemes (Rist et al. 2010; Luzar et al. 2011). However, hunting statistics often require some kind of correction for several sources of noise, namely, hunting effort and game management policies (Christensen 2005; Hörnell-Willebrand et al. 2006; Imperio et al. 2010; Ferreira et al. 2010; Willebrand et al. 2011; Pöysä et al. 2013). On the other hand, observation error in counts may be negligible at small spatial scale, given that application of census techniques can be more easily standardised locally, but at larger scale variability in environmental conditions (Sagarin et al. 2006), choice and application of techniques (Thomas 1996) and observer skills (Sauer et al. 1994) can remarkably affect population estimates. Furthermore, lack of repetitions in counts can lead to substantial stochasticity determining population estimates (Svensson 1979; Loison et al. 2006). These different sources of noise in counts and bags may eventually lead to inconsistencies between estimates (Imperio et al. 2010; Martinoli et al. 2017), although being based on the same populations. Hence, in such cases the integration of different observation processes within the same state process would minimise discrepancies taking advantage of all information available at the same time.

As already highlighted in the Introduction, no survey scheme to assess Alpine Galliforms at national scale has yet been implemented in Italy, and all information on population sizes are fragmented between game management authorities. Thus, the quality of the data available to assess species' status is rated as poor by BirdLife International (2015a), and still relies on approximate expert-based population abundance estimates (Brichetti and Fracasso 2004). Population trends based on these bags and counts have been shown not to be consistent for each species in the previous chapter, with species-specific issues arising for both counts and bags, mostly as independent detection errors.

Using the same dataset of Chapter 1, hereafter we present an efficient approach to join two different datasets on population abundance to reduce uncertainty on annual growth rates estimations at various spatial scales, taking advantage of all available information. More specifically, our study aimed at i) evaluating population trends of the three species at national, regional and site level, ii) checking if the estimated trends fit the current national Red list classification, iii) testing for an effect of game management policies on the datasets and iv) evaluating the performance of an integrated bags/counts model over single-proxy models.

2.2 Materials and methods

2.2.1. Study area

Data were collected from the whole Italian Alps, which host all BG and PTA national populations and roughly 75% of PAR populations (Peronace et al. 2012; Trocchi et al. 2016). Southern Tyrol (Bolzano/Bozen province) was excluded from the study due to data unavailability. The smallest geographical entity at which data were organized is the game management unit (GMU, average extent of 468±285 km^2), which corresponds to hunting districts in Western Alps or an aggregation of them in the Eastern Alps. In order to disentangle the effect of different game management schemes from biological factors on population trends estimates, we grouped GMUs according to two different categorizations. In the first one we grouped GMUs into ecological coherent areas, according to classification of the Alps into geographic sectors identified by Ozenda (1985), which takes into consideration elevation (inner/outer Alps), geology (silicaceous/carbonaceous soils) and geography (west-east gradient) (**Figure 2.1**). As for the second categorization, we grouped GMUs according to game management authorities, which may introduce noise through management policies, count methods and hunting effort. Depending on the GMU, we identified as game management authority the province, a group of provinces or the region, since in Italy hunting is entrusted to different administrative levels.

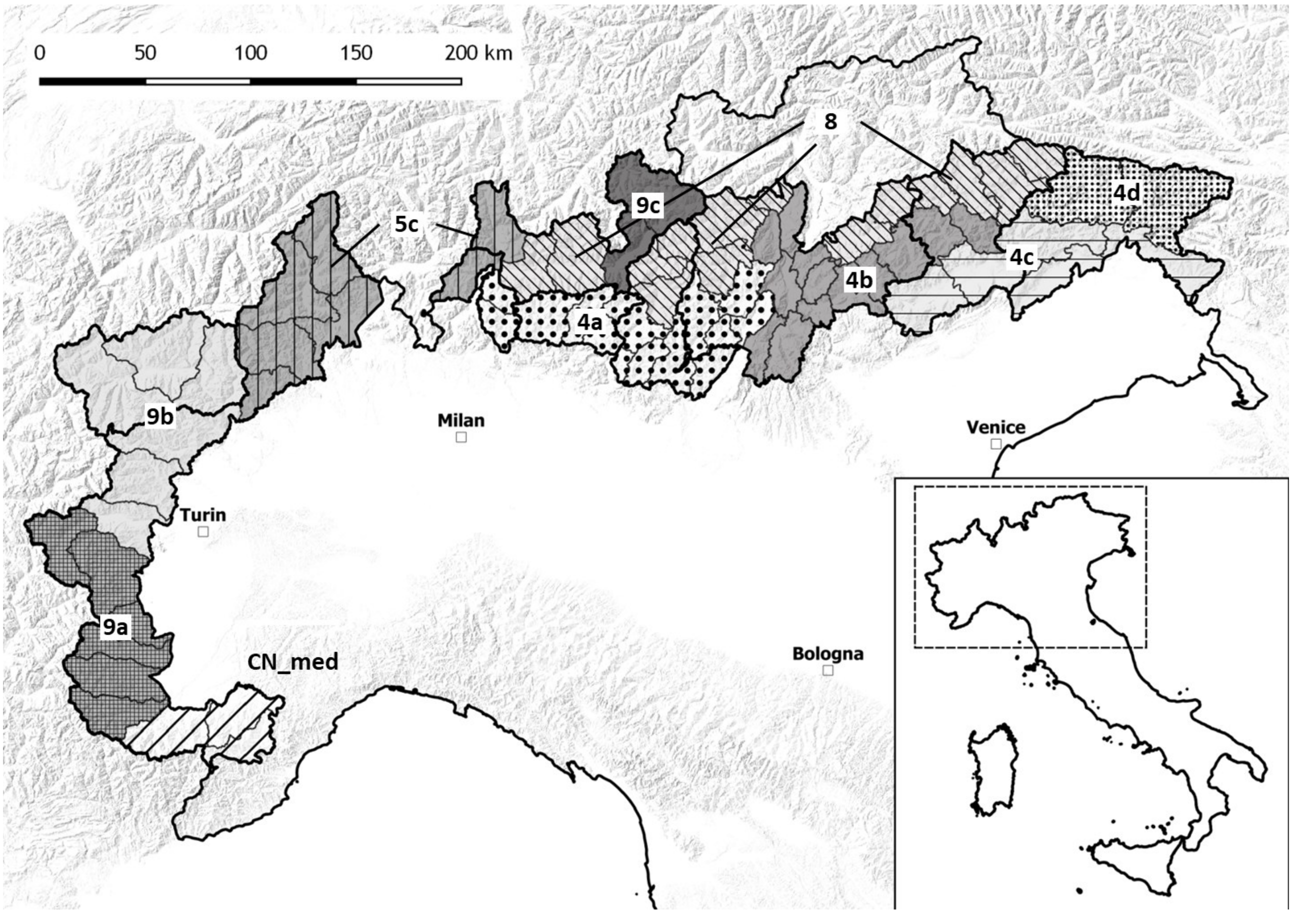


***Figure 2.1** – GMU (narrow black lines) and regional classifications of the study area. Thick black lines represent game management authorities, filling shades of gray/filling lines or dots represent biogeographic regions, as defined by Ozenda 1985*

2.2.2. *Count and bag data*

Populations are annually surveyed by game wardens and/or hunters to estimate breeding success through dog-assisted counts (Léonard 1992) with the aim to set a sustainable shooting plan. Since hunting management is delegated to local authorities (regions or provinces), counting effort is not standardized at national scale. Counts and game bags datasets were based on 19-year time series from 73 game management units (GMU) covering the whole Italian Alps (average GMU size, 468±285 km^2). Since PAR and PTA is allowed only in few areas, only BG data were available for each unit. Given that counts are mandatory in GMU which allow Galliform hunting, count and bag data were usually available for the same units. Series length are uneven across GMUs due to different archival policies of game management authorities and occasional hunting suspensions. On average, missing data represented 1/3 of the datasets, BG bags being an exception with only 11% missing values. Further details on data characteristics, on field methods applied for data collection and on hunting management can be found in Chapter 1.

2.2.3. Statistical analyses - integrated models

State-space models consist of a set of nested models, namely a model for the state process that describes the dynamics of the state (here population size, N, at each site *g* and time *t*) and a model for the observation process that links the observations (counts, y) to the state. This approach allowed us to take into account counting errors or imperfect detectability. State-space models offer the opportunity to deal with the expected large observation error by assuming that, on average, under- and overestimations cancel out. For post-breeding count data, this would correct for birds that go unnoticed (usually, lone adults) and double counts (flushed birds that move across different parcels). It can also adjust for random variations of sampling effort in time, which depend on weather conditions, number of surveyors/dogs, different skills of pointing dogs etc. For bag data, this would correct for failures in setting appropriate harvest rates or for weather conditions (e.g. early snowfalls in autumn) that displace birds from the usual shooting grounds or prevent access to them.

Despite the violation of the assumption of full independence of the datasets, which may result in overestimated parameter accuracy in integrated modelling, it was shown that the magnitude of this issue is negligible (Abadi et al. 2010a). Based on this premises, we modelled counts and bags as independent states, conditional on independent observation processes, sharing the same stochastic population growth rates.

We followed the approach described by Furrer et al. (2016), adapting it to the specific purpose of our study. More specifically, since our goal was related to the estimation of national and regional trends only, we did not address population synchrony and the effect of environmental variables, as decribed in the paper.

Usually, the state process model assumes an exponential population growth, where population size of each site *g* (represented in our case by GMU) at time t_{+1} is given by population size at time *t*, plus the growth rate $r_{g,t}$. For each of our datasets we built the same state model.

$$\log(Nc_{g,t+1}) = \log(Nc_{g,t}) + r_{g,t}$$

and

$$\log(Nh_{g,t+1}) = \log(Nh_{g,t}) + r_{g,t}$$

where *Nc* and *Nh* are counted and hunted population sizes. $r_{g,t}$ in our model is the link that allows the integration between bags and counts datasets. Observations (counts and bags) were modelled drafting from a log-normal distribution, allowing both over- and underestimations.

$$\log(c_{g,t}) \sim Normal\left(\log\left(Nc_{g,t}\right), \sigma c_g^2\right)$$

and

$$\log(h_{g,t}) \sim Normal\left(\log\left(Nh_{g,t}\right), \sigma h_g^2\right)$$

where $c_{g,t}$ and $h_{g,t}$ represent respectively, count and bag values. Observation errors are assumed to be site-dependent. Census effort is markedly different across GMUs in terms of number and size of sample areas, but within each GMU the effort remained the same. Because we are working on log-transformed data and focusing on population trends rather than abundances, the fact that sites exhibit different sizes has no impact on the results. Similarly, harvest rate did not change significantly over time, albeit changes in game management did occur, accordingly to an increased control on game management policies after the enforcement of the Natura 2000 network, which lead to more conservative harvest quotas in time (see Chapter 1).

Posterior probabilities of all model parameters are obtained applying Bayes' theorem to update the priors using the likelihood. Albeit the magnitude of the growth rates were already known from the previous study described in Chapter 1, we defined vague priors, except for the initial population size $\log(Nc_{g,1})$ and $\log(Nh_{g,1})$, for which we defined priors fitted to the range of datasets' values (see **Table S2.1** in Appendix 1).

Models were implemented in JAGS 4.2.0 (Plummer 2003) called from R using the package R2jags (Su and Yajima 2015). JAGS performs parameter estimation through Markov Chain Monte Carlo simulations (MCMC) by sampling the posterior distribution of the parameters. We ran 3 MCMC chains with 100000 iterations, discarding the first 50000 iterations as 'burn-in' (Gilks et al. 1996). Thinning was set to 9 for memory issues. Chain convergence was assessed both visually and by checking the Gelman-Rubin Rhat statistic (Rhat <1.1) (Brooks and Gelman 1998).

We performed a goodness-of-fit test, (Gelman et al. 1996; Kéry and Schaub 2012). For each dataset (counts and bags) we computed the ratio of the actual data and the mean of the generated values (both at log scale), as

$$\mathrm{w} = \frac{\log(y_{g,t})}{\mathrm{mean}\left(\log\left(z_{g,t,i}\right)\right)}$$

where $y_{g,t}$ represents the actual count or bag value and $z_{g,t,i}$ represents the generated count or bag value for each iteration i (being i[1,16668], resulting after burning and thinning). Data generation follows the observation model,

$$\log(z_{g,t,i}) \sim Normal\left(\log\left(Nz_{g,t,i}\right), \sigma_{g,i}^{2}\right)$$

Starting from the base integrated model, we implemented several different models to $r_{g,t}$, in order to examine population trends at various spatial scales.

2.2.3.1. Overall trend

In a first model we calculated a global growth rate μ to estimate a general trend at national scale.

$$r_{g,t} = \mu + \varepsilon_{g,t}$$

In this model we postulate the existence of an underlying common trend of all Italian populations and a component of the trend that is GMU specific, coded as $\varepsilon_{g,t}$, a normally distributed temporal random effect with a site—specific variance. Thus, $\varepsilon_{g,t} \sim Normal\left(0, \sigma_{glob}{}^{2}{}_{g}\right)$.The aim of this first approach was to provide an overview on the status of the target species in Italy, which is an important information when conservation policies are implemented at national or international scale.

2.2.3.2. Site-specific trends

In a second model we considered each GMU as an independent population. Relative to the previous model, we calculated a median growth rate μ_g as site fixed effect, as

$$r_{g,t} = \mu_g + \varepsilon_{g,t}$$

2.2.3.3. Regional trends

Third, we look for regional growth rates. As described before, we considered both a classification of GMUs based on game management authorities and a classification based on biogeographic zones. The aim was to explore whether growth rates calculated on these datasets could be acknowledged to biological factors or to different game management policies. We modelled $r_{g,t}$ as following :

$$r_{g,t} = \mu_{reg} + \varepsilon_{g,t}$$

where μ_{reg} is the mean regional growth rate (biogeographic or management). In order to check, we compared DIC (Deviance information criterion) values and precision of μ_{reg} values (95% Credible Intervals) calculated by models using the two regional grouping criteria.

2.2.3.4. Integrated vs classic approach

Similarly, in order to test the performance of the integrated model, we applied the site-specific model on both count and bag dataset separately and then we compared precision of μ_g calculated by the three models to check whether the integrated model did improve precision and bias of the estimation of Alpine Galliform population trends.

2.3 Results

Chains convergence was satisfactory in all models for every estimated parameter. *Rhat* resulted mostly <1.02, with no values passing the 1.1 threshold. For each considered model, the datasets generated using the model estimated parameters fitted the actual datasets with high precision. The posterior predictive check showed that the datasets calculated a posteriori from the model estimated parameters $\log(Nz_{g,t,i})$ and $\sigma^2_{g,i}$ were largely similar to the actual datasets, with a mean actual-to-generated data ratio always comprised between 0.90 and 1.00, indicating a slight overestimation of the generated data, especially for bag data.

Sample size affected species' growth rate parameter precision, despite median values of mean growth rates at different scales were similar (**Figure 2.2**). In fact, 95% CI width were smallest for the global growth rate μ (sample size: BG, 2736; PAR: 1900; PTA, 1100) and, on average, largest for the site growth rates μ_g (mean sample size per site: BG, 26.1; PAR: 25.8; PTA, 25.8). Intermediate values were recorded for the regional growth rates μ_{reg_g} (mean sample size per region, biogeographic/authority: BG, 182.4/202.6; PAR: 126.1/157.6; PTA, 106.4/49.0).

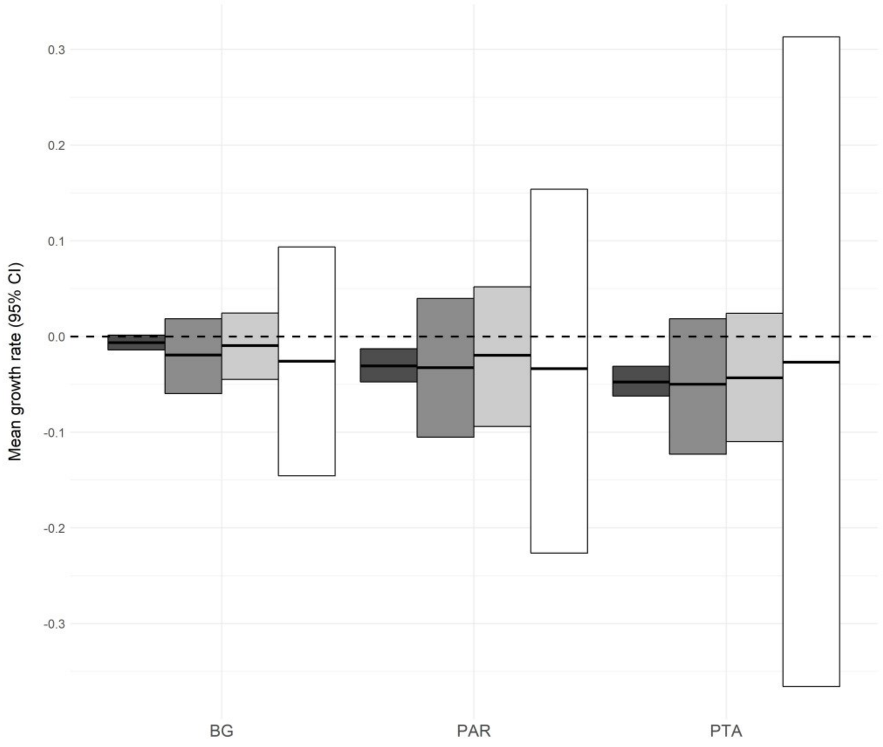


Figure 2.2. *– Precision of mean growth rate parameter µ in the different models (mean and 95% CI) estimated by the different models for the three target species (BG, Black grouse; PAR, Rock partridge; PTA, Rock ptarmigan), relative to the period 1996-2014. Models are represented with different shades of gray. Dark gray = global µ; intermediate dark gray = mean regional µreg (authority); light grey = mean regional µreg (biogeographic); white = mean site µg)*

Table 2.1 *– Posterior estimated mean growth rates, 95% CI, estimated population change and DIC for the three target species (BG, Black grouse; PAR, Rock partridge; PTA, Rock ptarmigan) as estimated by the different models from 1996 to 2014. For site and regional models, displayed values refers to the mean values of single sites or regions.*

species	model	posterior µ median		lower 95% CI		upper 95% CI		95% CI interval		P(µ<0)		% change across 1996-2014		DIC
			mean		*mean*		*mean*		*mean*		*mean*	*mean*	*95% CI*	
BG	global	-0.006		-0.014		0.002		0.016		0.90		-10.59	-22.55, 2.73	2044.8
	site		-0.026		-0.145		0.094		0.239		0.61			2216.8
	regional - biogeographical		-0.009		-0.045		0.024		0.069		0.65			6346.6
	regional - authority		-0.019		-0.060		0.019		0.078		0.76			6132.2
PAR	global	-0.031		-0.047		-0.013		0.035		100.00		-42.95	-58.28, -20.84	2263.1
	site		-0.034		-0.226		0.154		0.380		0.60			2239.4
	regional - biogeographical		-0.020		-0.094		0.052		0.146		0.64			6262.6
	regional - authority		-0.032		-0.105		0.040		0.145		0.73			6255.9
PTA	global	-0.047		-0.062		-0.031		0.031		100.00		-58.28	-68.46, -43.48	1339.6
	site		-0.027		-0.366		0.313		0.679		0.54			1336.6
	regional - biogeographical		-0.043		-0.110		0.024		0.134		0.82			3152.4
	regional - authority		-0.050		-0.123		0.019		0.142		0.87			3030.0

2.3.1. Overall trend

The first model estimated a negative trend at national scale for all three target species from 1996 to 2014. The median decrease of BG populations was estimated at less than 1% (μ = -0.006), but a fraction (12.5%) of 95% CI interval was positive (min -0.014, max +0.002). For both PAR and PTA the trend resulted instead negative (respectively, PAR, μ = -0.031, CI 95% min -0.048, max -0.013; PTA, μ = -0.047, CI 95% min -0.062, max -0.031). The mean change of population size over the study period was -11% for BG, -43% for PAR and -58% for PTA.

2.3.2. Site-specific trends

Consistently with the overall trends, all species showed negative growth rates on average at site level in the integrated model (BG: 71% of the sites, n=72; PAR: 70%, n=50; PTA: 80%, n=30). Nevertheless, only in few cases growth rates values were significantly different from 0 (BG: no sites; PAR: 1 site; PTA: 3 sites.

In the integrated model bags resulted more subject to observation error than counts, as evidenced by the comparison of σc_g^2 and σh_g^2 (**Figure 2.6**). Simlarly, highest observation error was detected in PTA and lowest in BG, with PAR showing intermediate values.

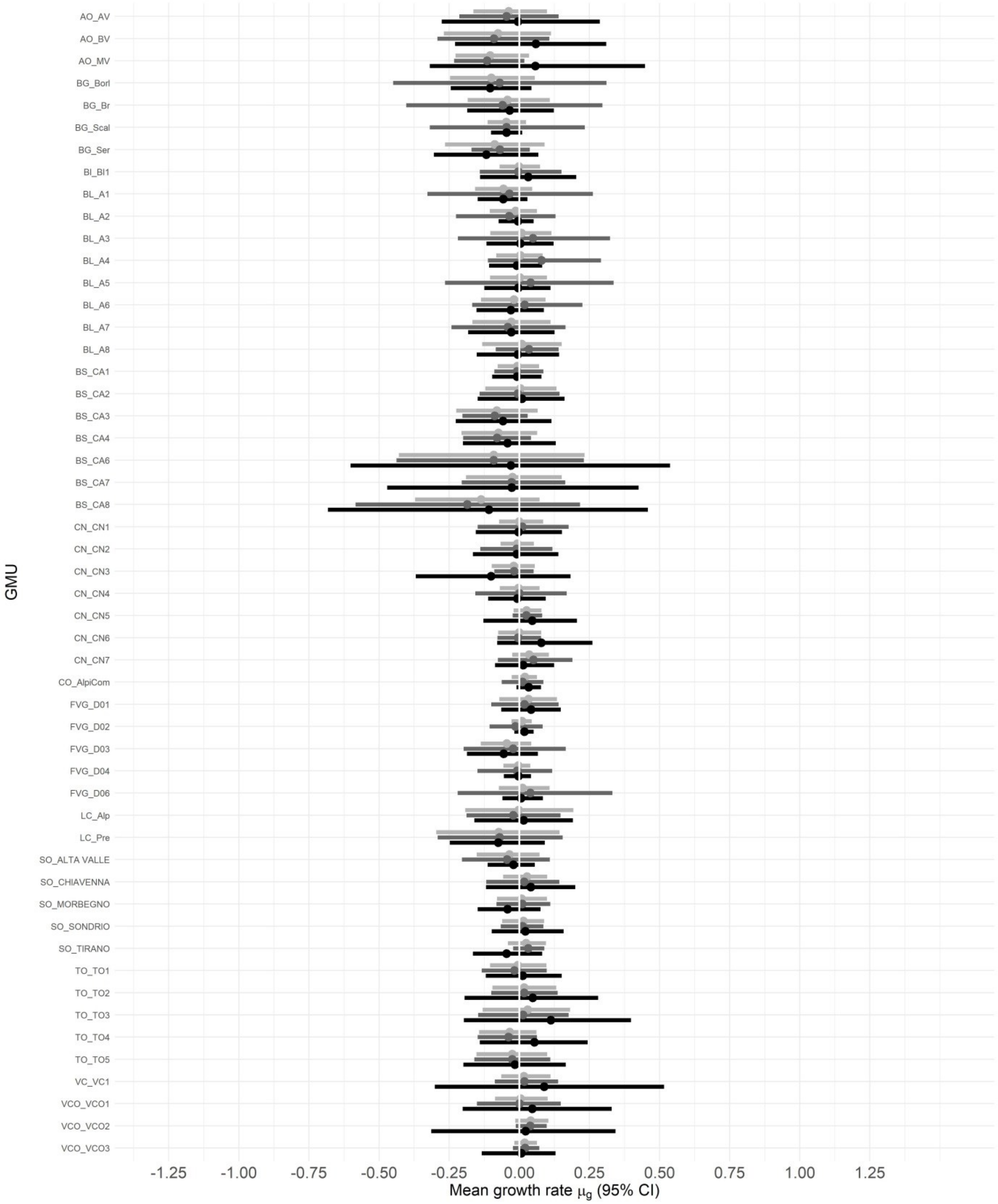


***Figure 2.3** – Mean Black grouse growth rates in GMUs and 95% CI estimated from 1996 to 2014 for each site. Light gray: integrated model; intermediate gray: bag-based model; black: count-based model.*

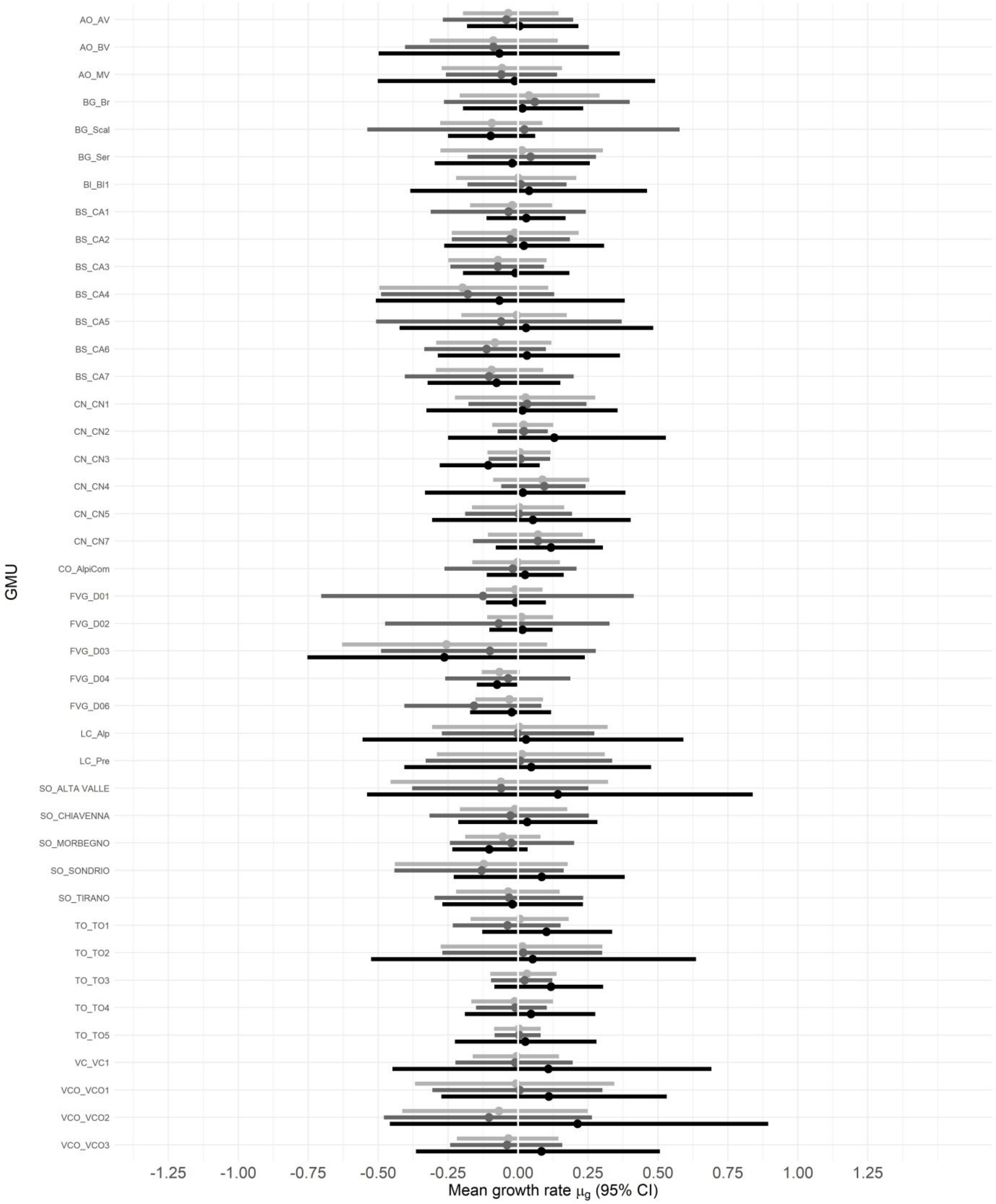


Figure 2.4- *Mean Rock parteidge growth rates in GMUs and 95% CI estimated from 1996 to 2014 for each site. Light gray: integrated model; intermediate gray: bag-based model; black: count-based model.*

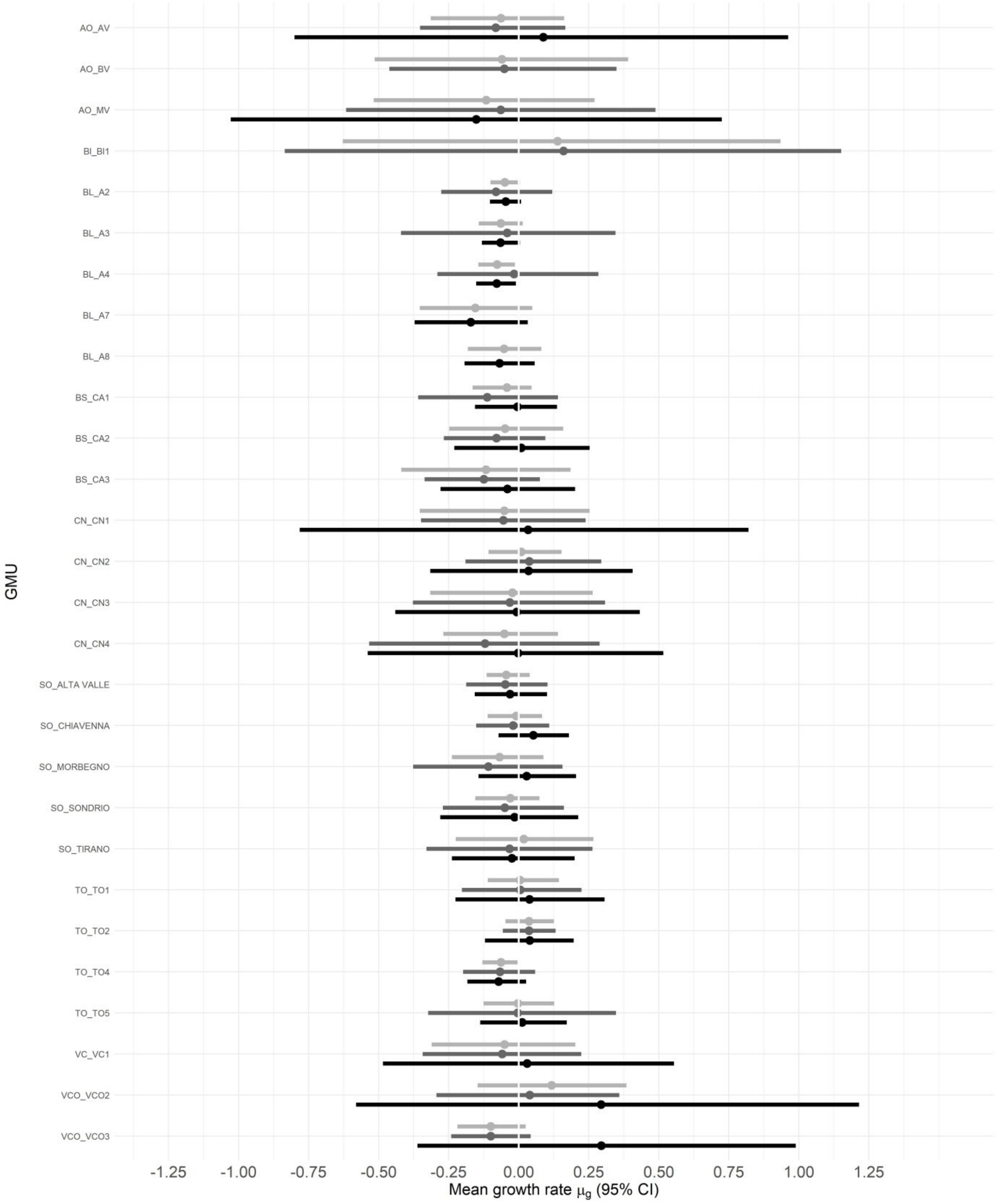


Figure 2.5- *Mean Rock ptarmigan growth rates in GMUs and 95% CI estimated from 1996 to 2014 for each site. Light gray: integrated model; intermediate gray: bag-based model; black: count-based model.*

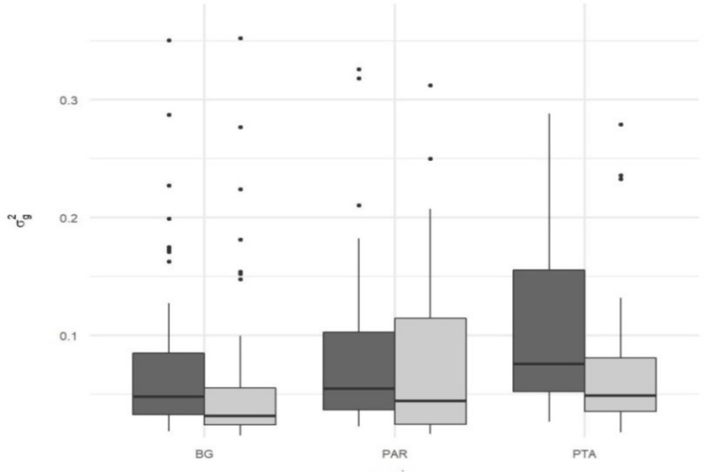


Figure 2.6 *– Mean of the site-specific variances of the observation models for the three target species (BG, Black grouse; PAR, Rock partridge; PTA, Rock ptarmigan). 25-75% interquartile range (IQR) is delimited by the box, whiskers extend to 1.5 IQR. Dark gray refer to bags observation models, light gray to counts observation models.*

2.3.3. Regional trends

Grouping sites according to game management authorities or biogeographic regions only marginally affected regional growth rate estimations. In fact, both DIC model values and 95% CI intervals were similar (**Table 2.1**). Hence, the results of regional-effect models do not support the hypothesis that game management affects population size estimates, albeit lower DIC values of the authority-based models may anyway hint at a possible effect of management policies. Looking at the estimated biogeographic regional trends for BG, a W-E gradient emerges for populations of Central-Eastern outer Alps (regions 4a to 4d), with significantly declining populations in western GMUs and progressively higher growth rates going east. Higher growth rates are recorded in the inner Alps (9c, 5c), but it must be noted that a positive trend is also recorded in the southernmost biogeographic region (CN_med), characterized by submediterranean habitat elements. PAR populations are declining mostly in the Central-Eastern Alps (4a, 4b,4c, 8, 9c), while stable or increasing populations are located in the Central-Western (5c, 9a, 9b, CN_med) and Eastern Alps (4d). Less variability between regions results for PTA instead, whose populations are all declining with a mean annual rate in the range 3.3-7.2%, with the Cottian Alps being the only exception (annual growth +0.4%).

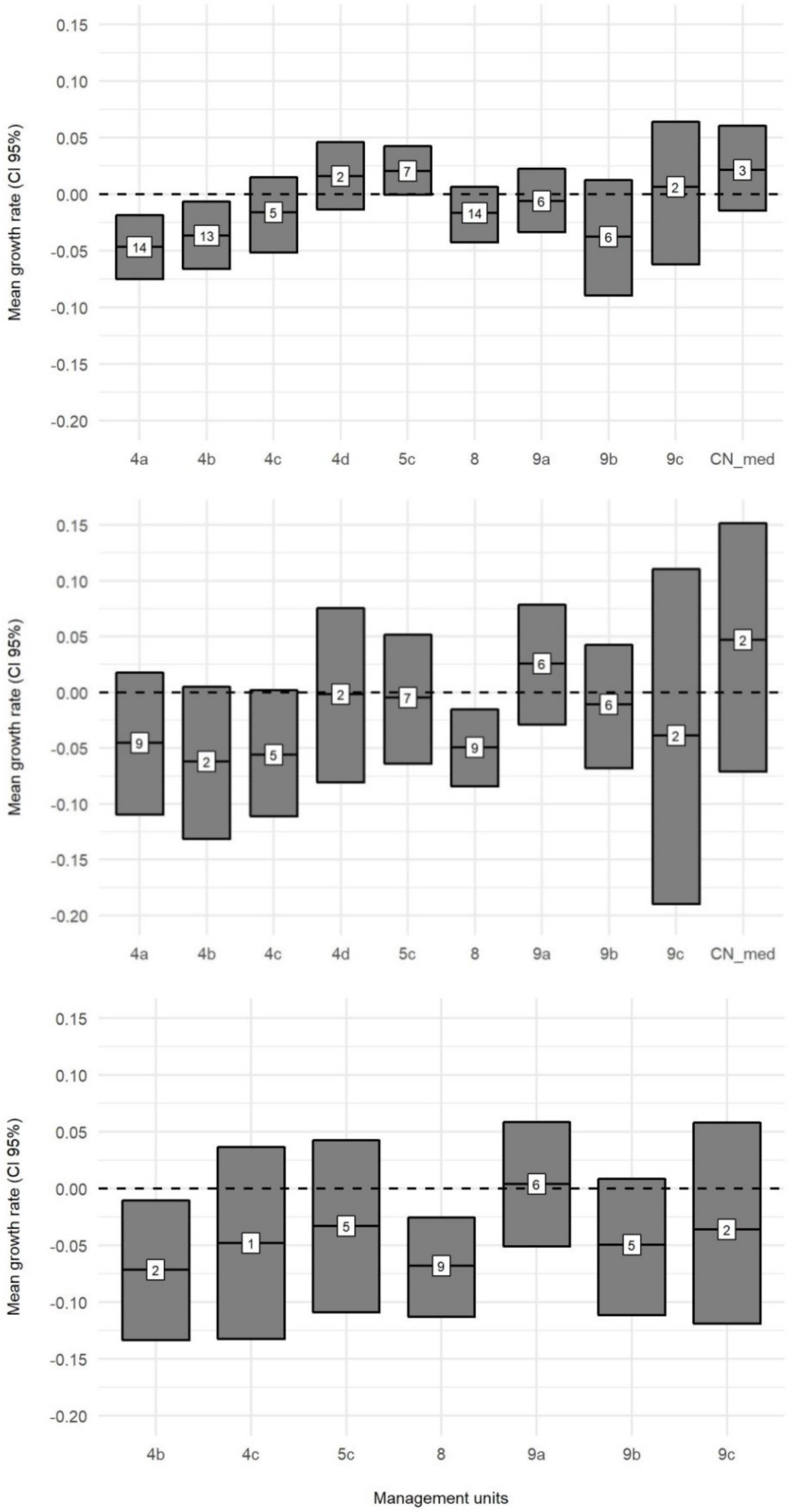


Figure 2.7 *– Regional (biogeographic) growth rates (mean and 95% CI). Upper: Black grouse; middle: Rock partridge; bottom: Rock ptarmigan.*

2.3.4. Integrated vs single-proxy models

Integrating counts and bags within the same model led to a more precise estimation of site mean growth rates μ_g, by comparing 95% CI width with the single-proxy models. The integrated model led to reduction in the median CI width of μ_g estimates from 0.402 to 0.269, For the three species BG, PAR and PTA, the integrated model was more accurate, respectively, in 65% (n=52), 40% (n=48) and 75% (n=28) of the sites. Since count and bag data were not available for all authorities, this comparison was implemented only for a subset of sites.

Precision of μ_g estimates, both in the integrated and in the single-proxy models, was related to several factors, most notably the sample size (i.e data series lengths), the absolute value of μ_g and the magnitude of counts and bags (**Figure 2.8**). CI width declined sharply with an increase in data series length, which spanned from 5 to 20 years across species and proxies. For each site, sample size in the integrated model spanned from 11 to 40 years, which helped the integrated model in estimating growth rates more accurately using a larger dataset. It must be noted, however, that the relation of sample size and precision of the growth rates estimates is not linear when CI of μ_g estimates from single-proxy and integrated models are pooled. In fact, the integration of two short data series of counts and bags led on average to a less accurate estimate compared to a longer series of a single proxy. Deviations from stability of the growth rates, either they increased or declined, resulted in wider CI. Conversely, growth rates were more precisely estimated when they only marginally deviated from 0. Finally, precision was inversely related to the magnitude of counts and bags values, with wider CI associated with smaller values.

In most cases (BG, 86%; PAR, 74%; PTA, 75%), growth rates estimated by the integrated model were intermediate between count-based and bag-based models growth rates.

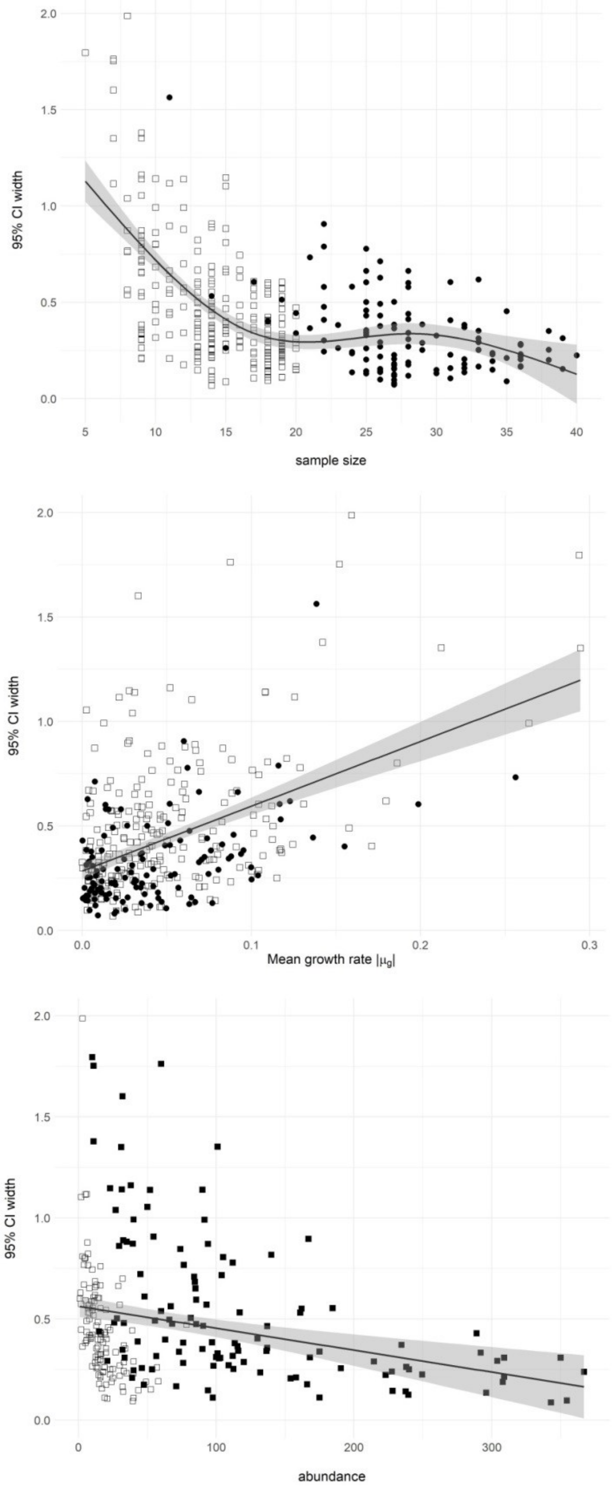


Figure 2.8 – *Relation between precision of site growth rates μ_g (expressed as 95% credible intervals width) and factors. Top: site data series length (sample size). Empty squares represent either count or bag series at site level, black dots represent integrated series (hence, the sum of count and bag sample size for each site). The smoothing line was calculated by a Generalized Additive Model (GAM) with k=4. Middle: mean site growth rates μ_g, expressed as absolute values. Empty squares represent either count or bag series at site level, black dots represent integrated series. Bottom: median magnitude of count (white squares) and bag (black squares) values.*

2.4 Discussion

2.4.1. *Advantges of integrating counts and bags*

In this study we outlined how to integrate two different proxies of population abundance robustly. One of the goals of our work was how to make the best of all available data, considering the current enforced game management, especially in terms of reducing uncertainty in parameter estimation by improving precision and reducing bias. Uncertainty is a crucial aspect in ecological modelling (Pradel 2005), especially in wildlife management and conservation (Nichols et al. 1995; Williams et al. 1996; Johnson et al. 1997; Williams et al. 2002; Regan et al. 2005). Large credible intervals of estimated population dynamics parameters are ill-suited to make reliable inferences. This may be particularly relevant, for example, when adaptive management is applied (Nichols and Williams 2006). According to Williams et al. (2002), four main sources of uncertainty can be identified in wildlife management, among which they mention the application of different monitoring methods to the same target species. As already outlined in the Introduction and Chapter 1, this issue is extremely relevant in the context of the estimation of population trends of Alpine Galliforms. More specifically, the two analysed datasets of counts and bags were composed of game management units annual data series deriving from different counting methods/effort, uneven hunting policies and data archival. As a consequence, the datasets were heterogeneous in terms of series length and magnitude of count and bags values.

All this considered, the integration of the two proxies within the same model was a useful approach that helped increasing precision and limiting bias of the growth rates estimates. We detected two factors that affected the quality of the available data to modelling purposes, that is, the series length and the magnitude of the values. Larger credible intervals in single--proxy site models were associated to short series and/or to small values. In most cases, bag series were longer than count series, as a result of a widespread lack of standardization of census methods and data archiving. Conversely, as expected, the magnitude of counts usually far exceeded the magnitude of bags (median value counts/bags: BG, 156/18; PAR, 87.7/14,5; PTA, 39.2/8.5), leading to more accurate parameter estimation. Hence, the integrated model increased precision of growth rates estimates by mutually compensating proxy-specific shortcomings. The limited magnitude of bag values was found being particularly relevant. Unexpectedly, the error in the bag observation model was higher than the error in count observation model, despite the magnitude of count values being larger than bags. Similarly, the observation error was highest in PTA and lowest in BG, albeit both count and bag values being far smaller for PTA than BG. This counterintuitive outcome was likely caused by a failure of the model in dectecting accurately year-to-year population abundance variations when dealing with very small values, such as PTA bags, which were in the range of units. As a consequence, site growth rates estimates precision was lowest in PTA and highest in BG.

At all spatial levels (global, regional, site) the integration of counts and bags in this case helped limiting very large 95% CI. In fact, the overall growth rate parameter μ was estimated precisely, relying on a considerable amount of data to source information from, while 95% CI width increased remarkably in regional and site models as the sample size reduced. It is interesting to note that the integration succeded in averaging both proxies weighting them by their own quality (series length * values magnitude). For each site, growth rates estimated by the integrated model resulted closer to the ones estimated by the proxy with highest quality, which changed among sites according to the different wildlife management policies.

In Chapter 1 we discussed about proxy-specific sources of bias. Bags trends are likely underestimations, since game management changed from less to more conservative from mid-2000 on, especially after the enforcement of Natura 2000 network, that resulted in reduced harvest rates. Furthermore, there is an unknown poaching quota, not recorded in shooting bags. Conversely, we speculate that counts may overestimate population abundances, considering that the sampling areas are usually located in the best habitats where the encounter probability is higher. Moreover, in regions where hunters are running the counts and game wardens only occasionally supervise, shooting plans could be biased by intentionally inflated results, aimed at getting higher yields. For most sites, growth rates estimated by the integrated model resulted intermediate between growth rates estimated by count-based and bag-based models. Therefore, the use of state-space models, which intrisically buffer the sources of bias by accounting for the observation error, combined to the integrated approach, may help also in reducing bias in growth rate estimates by averaging the information brought by the two proxies.

This study confirms the strength of the integrated models in reducing bias and increasing parameter estimation precision out of limited or poor quality data, already shown in the last decade by several studies (Schaub et al. 2007; Abadi et al. 2010a; Davis et al. 2014). We would recommend that the various authorities in charge of wildlife management in Italy consider this integrated approach when implementing management strategies, besides the obvious need to improve quality of the primary data, chiefly, by an increase in count methods standardisation.

2.4.2. National and regional trends

For the three species of Alpine Galliforms considered, the results of our study confirm the status assigned by the latest version of the national Red list of birds (Peronace et al. 2012), that is, 'Least Concern' (LC) for the BG, and 'Vulnerable' (VU) for PAR and PTA. On a 19-year basis, BG Italian population marginally declined (-11%, median estimate) and this reduction do not meet the IUCN criteria for a 'Near Threatened' (NT) classification, despite some sharp declines at regional level (i.e. Central Alps prealpine areas) have been occurring. For PTA and PAR, if the estimated 19-year growth rates would be applied to 10 years (the reference period for IUCN classification, IUCN 2001), the size of the population decline would meet the criterion A2 ("population size reduction of ≥ 30% over the last 10 years*"*) for the former (-38%) while the latter would approach to it (-27%). In case of PAR, it must be noted the an estimated 30-50% of the Italian population was not considered in this study, since it lives in the Apennines and in Sicily (BirdLife International 2015d), where the local subspecies (sspp. *A. g. graeca* and *A. g. whitakeri*) have faced a severe reduction in the last decades (Palumbo and Lo Valvo 1999; Rippa et al. 2011; Sorace et al. 2011, 2013a, b; Trocchi et al. 2016).

The comparison between species' national growth rates estimated by TRIM in Chapter 1 and the ones estimated by the integrated model are partly overlapping, and some species-specific differences emerged (**Figure 2.9**). As already outlined in Chapter 1, BG count and bag population trends are remarkably different, likely resulting from changes in game management policies in time. However, the integrated model estimated an intermediate trend value, which largely overlapped with the counts anyway. This result is consistent with a prominent effect of the magnitude of counts values over bag values, given that, at national scale, the issue of shorter series length of count data at site level was largely attenuated. PTA count and bag trends were consistent in the log-linear frequentist appproach, and the decline predicted by the integrated Bayesian model resulted only marginally less severe. A substantial difference between the outputs of the two approaches emerged for PAR, for which the integrated model estimated a shaper decline compared to TRIM. As already suggested in Chapter 1, TRIM may have failed in correctly identifying long-term PAR population trend due to the presence of ample population fluctuations. The decomposition of the year-to-year growth rates into a global mean and a site/time error with a site fixed effect in the state-space integrated model may have contributed in reducing the bias introduced by few sites with large absolute count values showing a positive trend (i.e. a site in Central Alps which shares on average a 10-20% quota of the whole number of counted birds)

Examining in depth the trends in different biogeographic areas, populations of inner and Eastern Alps seems to perform better than populations living in the pre-Alpine belt and Western Alps, as a likely effect of marginality and fragmentation of populations. Indeed, the main core of BG distribution on the Alps lies in the inner Alps, where there is a continuum of suitable habitats. In the pre-Alps, populations are instead more fragmented and usually live at lower densities (Brichetti and Fracasso 2004). Although birds populations are less affected by fragmentation than other vertebrates (Crochet 2000), BG is a highly resident and philopatric species (Caizergues and Ellison 2002) with southern populations being more fragmented than northern (Caizergues et al. 2003b). This may affect populations' fitness. We speculate that the observed W-E gradient may be explained likewise, given that Eastern Alps are characterized by lower mountain ridges and populations living there are neighbouring the Austrian ones. Less clear regional patterns resulted for PAR and PTA, although Western populations performed better in both species. For these species, the effect of local conditions may be stronger than larger scale environmental dynamics, as already observed for other Alpine populations (Géhin and Montadert 2016; Furrer et al. 2016), hence geographical patterns of trends can hardly be identified.

The effect of different game management on the dataset remains an open question. We could not find a strong evidence that management policies diversity affects the trends, despite the results in Chapter 1 have previously shown the existence of different game management policies (i.e. hunting pressure), which were likely causing significant different trends between game management authorities. In this second study, we tried to disentangle management from environmental effects, but the inevitable overlap between the two classifications may be a confounding factor. The lack of management guidelines in some authorities may have resulted in a high within-authority differences among sites (chiefly, in Lombardy region), which prevent the identification of common patterns. On the other hand, the prevailing effect of local conditions over larger scale environemental factors, as abovementioned, could have prevented the identification of regional patterns.

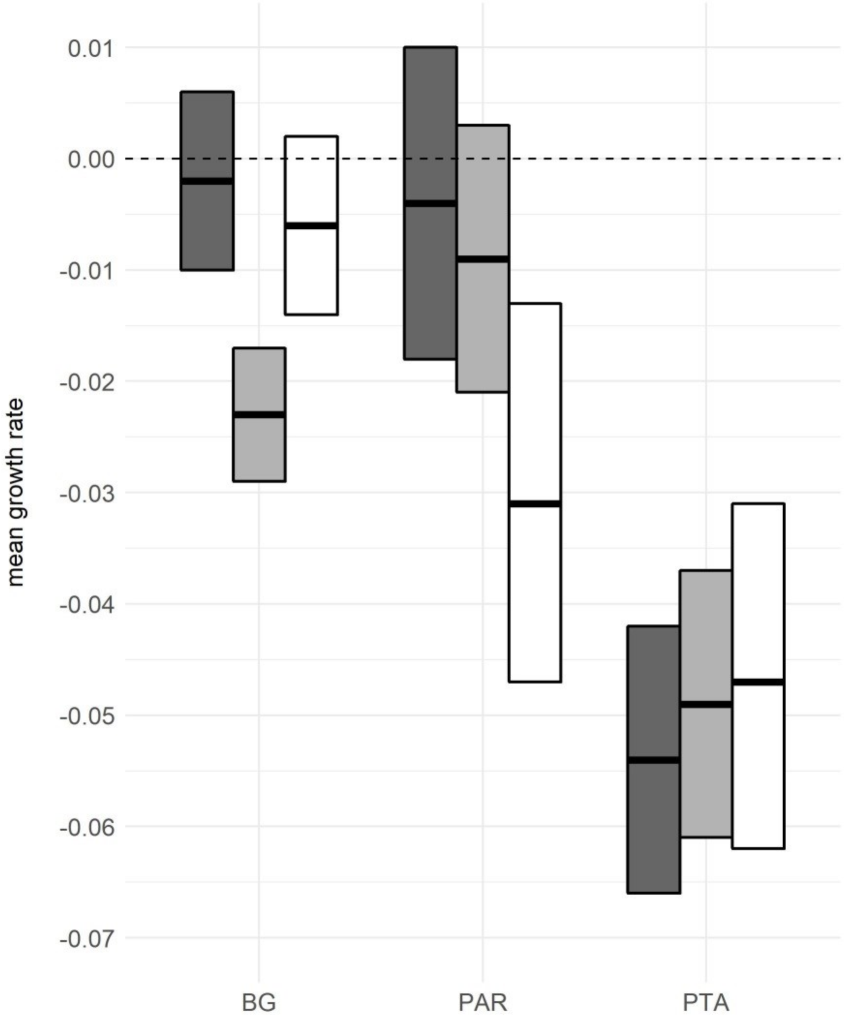


Figure 2.9 *– Comparison between national growth rates estimated in Chapter 1 using TRIM from count (dark gray) and bag data (light gray) and the mean growth rate estimated by the integrated model (white) for the three target species. Crossbars show the mean growth rate μ and the lower and upper 95% credible intervals for the integrated model, while for the results of TRIM crossbars show the trend values estimated by the log-linear models and the lower and upper 95% confidence intervals.*

2.4.3. Applications of the integrated model

As long as there is no focused monitoring scheme to assess the abundance in time of Alpine Galliforms populations at national level, the process of estimating population dynamics will necessarily rely on heterogeneous data that are routinely collected from the field. This issue is commonplace in wildlife management at large scale, because spatial variation of applied survey methods if often considerable (Pollock et al. 2002). As already mentioned, a major advantage of this approach is the possibility to limit uncertainty in parameter estimation by increasing sample size, joining different data sources within the same framework. This model could be applied when different methodologies are involved to get abundance estimates of the same populations at the same temporal frame according to the eco-ethology of the target taxon. For example, gregarious species with commuting behaviour, such as bats, seabirds (cormorants, auks etc.), herons or corvids, are usually surveyed at roosting/breeding sites and foraging areas (see Bibby et al. 2000; Agnelli et al. 2006). In these cases, integrating data could result in more robust trends estimations, given that small or newly established colonies may go undetected and variability in the use of foraging areas for certain species is extremely high depending on food availability and weather conditions (Legagneux et al. 2009). The scope of application could be widened to direct and indirect count methods, where abundance indices (snow tracks, faeces, feeding signs etc.), obtained from cheap large scale surveillance surveys, can be coupled with intensive direct targeted monitoring. The flexibility of state-space models further allows an easy dataset integration without putting many assumptions on their relationship. Indeed, each biasing factor that affects data can be independently accounted in the observation processes, such as detectability (Royle et al. 2005), weather conditions (see for example droppings residence time in faecal pellets counts, Wallmo et al. 1962), sampling effort (Willebrand et al. 2011) or fieldworker skills (Sauer et al. 1994).

2.5 Appendix 1

Table S2.1 *–Specification of the prior distributions for the parameters in the models*

MODEL	PRIOR
All models	$\log(Nh_{g,t1}) \sim \text{Uniform}(-5,6)$
	$\log(Nc_{g,t1}) \sim \text{Uniform}(-5,10)$
	$\varepsilon_{g,t} \sim \text{Normal}(1, \sigma^2_{proc})$
	$\sigma_{proc} \sim \text{Uniform}(0,10)$
	$\sigma h^2_g = \mu\sigma h^2_g + \varepsilon\sigma h_g$
	$\mu\sigma h^2_g \sim \text{Uniform}(0,1)$
	$\varepsilon\sigma h_g \sim \text{Normal}(1, 1000)$
	$\sigma c^2_g = \mu\sigma c^2_g + \varepsilon\sigma c_g$
	$\mu\sigma c^2_g \sim \text{Uniform}(0,1)$
	$\varepsilon\sigma c_g \sim \text{Normal}(1, 1000)$
Global	$\mu \sim \text{Normal}(1, 1000)$
Site	$\mu_g \sim \text{Normal}(1, 1000)$
Regional	$\mu_g = \mu_{reg} + \varepsilon\mu_{regg}$
	$\mu_{reg} \sim \text{Normal}(1, 1000)$
	$\varepsilon\mu_{regg} \sim \text{Normal}(1, 1000)$

Chapter 3

Land cover/land use changes disrupt Black grouse (Lyrurus tetrix *L.) habitat suitability: differential effects between inner and outer Alps*

ABSTRACT. In this Chapter we focused on Black grouse habitat changes caused by land abandonment in a 35-year temporal scale in the Central Alps. Shrub encroachment and forest ingrowth into former pastures and hay meadows is known to be detrimental to the species, as vegetation densification alters the optimal structural composition, where all vegetation layers (herbs, shrubs, trees) are present in a patchy layout. Using a georeferenced dataset of display sites dating back to the early 1980s, we modelled the past species distribution using land cover and landscape structure information obtained from land cover maps and remote sensing and we compared it with the actual distribution predicted by the model with current land cover. Overall, Black grouse habitat suitability distribution related to land cover halved in the considered period. Change occurred primarily in abandoned wood pastures and hay meadows. However, the change was not uniform in the study area, as a large proportion of habitat loss was located at low elevations in the outer Alps and only minor changes occurred in the inner Alps. This scenario is consistent with the different timing of farming and traditional activities discontinuation, which started right after WWII ending in the Prealps while this process was delayed in the inner valleys to the 1970s-1980s. At landscape level, the study outlined a deep habitat fragmentation into smaller patches of suitable habitat formely merged into a matrix of suboptimal areas, which will likely affect the species conservation by increasing edge effects. Despite not considering other factors that shapes the ecological niche (climate, predation, disturbance), the study evidenced that habitat management is needed to mitigate the negative effect of land abandonment on Black grouse populations.

KEYWORDS: Species distribution models, LULCC, land abandonment, Black grouse, conservation

3.1 Introducion

Land abandonment is a widespread phenomenon observed in many parts of Europe, both in lowlands and mountains (DLG 2005; Plieninger et al. 2006; Renwick et al. 2013). Land use/land cover changes (LULCC) are considered to be major drivers behind changes in ecosystem function and dynamics (Cernusca et al. 1999). Reduced grazing and haymaking causes a vegetation succession occurring at varying rates depending on site conditions which leads to densification of shrub cover and reforestation (Tasser and Tappeiner 2002). Biodiversity loss is first seen in vegetation due to increased competition for light and seed germination (Grime 2006) and eventually affects animal communities (Burel and Baudry 1995; Laiolo et al. 2004; Koch et al. 2015). Even though climatic warming will likely exert a major influence in the future on Alpine treeline, given that treelines are temperature-controlled boundaries (Körner and Paulsen 2004), at shorter time scales land use changes have been shown to act as main drivers of the observed upward shift (Dullinger et al. 2003; Gehrig-Fasel et al. 2007; Chauchard et al. 2010). Indeed, treeline position is believed to lag behind climatic changes by at least 50 years, due to recruitment lags, slow tree growth and competition with faster-growing shrub layer (Dirnböck et al. 2003; Harsch et al. 2009; Körner 2012). For example, a mere 4% of recent forest expansion observed in Switzerland is attributed to climatic treeline advancement, with the remainder 96% identifiable as gap-filling (Gehrig-Fasel et al. 2007), a process that is yet to be concluded where land use exerted a major control on treeline in the past (Vittoz et al. 2008). Historically, anthropogenic treelines on the Alps were estimated to be 150-300 m lower than natural treelines (Holtmeier and Broll 2005; Wallentin et al. 2008). However, climate warming interacts with land use changes by speeding up vegetation densification triggered by land abandonment providing better conditions for shrubs and forest growth and shifting upwards the climatic treeline, thus widening the potential expansion area (Bolli et al. 2007; Leonelli et al. 2011; Tasser et al. 2017). Dwarf shrub invasion represents the first observed step of the ecological succession and occurs at considerable high rate right after haymaking is discontinued. Nevertheless, scrubs are in most cases just an intermediate phase of the ecological succession and shrub cover on the long run is substituted by forest cover up to the climatic treeline (Tasser and Tappeiner 2002; Tasser et al. 2017), provided geomorphological and microtopographical constraints (Leonelli et al. 2011).

Farming discontinuation and forest expansion is considered the most relevant LULCC in Italy from 1940 to 2000 (Piussi and Pettenella 2000). An estimated 800,000 ha of pastures and hay meadows were abandoned in whole Italian Alpine slope from 1960 to 2000 (Chemini and Giannelle 1999). First evidences of forest expansion induced by reduced grazing pressure dates back to the early 1930s, which eventually became more intense from the 1960s (Motta et al. 2006). A 115 m upward treeline shift in Western Italian Alps was observed in the 20th century, and has the potential of a further 110 m shift (Leonelli et al. 2011).

As already highlighted in the thesis Introduction, LULCC have been shown to play an important role for Black grouse conservation. Nevertheless, few studies have directly addressed the question of how land abandonment is affecting the potential distribution of the species and none to our knowledge concerns Italy.

Local extinctions and distribution shrinking of Black grouse were observed in the Alps since the 1950s (De Franceschi 1994; Buffet and Dumont-Dayot 2011) at least partly as an effect of land cover (Ellison and Magnani 1985; Bernard-Laurent 1994b). Although the species distribution in Switzerland is virtually unchanged from the period 1973-1976 to 2013-2016 (Knaus et al. 2011), upward displacements of leks are reported in Valais Canton from 1970 following the treeline altitudinal shift (Marti et al. 2016). In Southern Switzerland, reduced breeding success and negative population growth rates were attributed Green alder expansion in pre-Alpine pastures (Zbinden et al. 2003). Land abandonment and consequences of land cover changes to biodiversity have been reported also on the Italian Alps and the Apennines (Farina 1991; Laiolo et al. 2004; Falcucci et al. 2006; Sergio and Pedrini 2007; Marini et al. 2011), but no studies have been conducted so far in Italy to evaluate effects on Black grouse habitat suitability, especially in the light of the different landscape evolution and abandonment history of the outer Alps belt, which experienced the discontinuation of traditional farming yet in early 20th century, and the inner Alps, where this phenomenon occurred later and slower.

In this study we analysed Black grouse habitat suitability distribution changes in Central Italian Alps from the early 1980s to present related to LULCC, using both land use maps and remote sensing techniques. More specifically, we applied SDMs (species distribution models) to evaluate i) the magnitude of habitat suitability change, ii) the existence of different patterns of change between inner and outer Alpine belts, iii) changes in habitat configuration at landscape level and iv) robustness of remote sensing-derived indices to identify Black grouse habitat.

3.2 Materials and methods

3.2.1. Study area

The area of interest is represented by the Alpine and pre-Alpine part of Lombardy region, located in Northern Italy. Area size is roughly 10000 km^2, with an elevational range between 200 and 4020 m asl (Piz Bernina) and it shares the northern border with Switzerland (Grisons and Ticino Cantons), which runs for most of its length along the main Alpine watershed. Two main zones are identifiable within the area separated by the so-called “Insubric line”, the local section of the Periadriatic seam, a major tectonic fault that separates the Adriatic from the European Plate trending E-W along Valtellina and upper Valcamonica. Northern Rhaetian Alps (hereinafter ‘inner Alps’) are located north of the line, characterized by higher elevations, steeper slopes and continental climate, while south of the line lie the Orobie Alps and the Southern Rhaetian Alps (hereinafter ‘outer Alps’), with wet climate and lower elevations that eventually end in pre-Alpine foothills. Treeline elevation is not uniform and it varies from 1200 m in the outer Alps, where it was historically lowered by human activities, up to 2400 m in the inner Alps. Consequently, Black grouse throughout the year can be found from 1000 up to 2600 m, living in broadleaved (chiefly, Beech, *Fagus sylvatica* L.), mixed or conifer sparse woods, despite most of the observations are found between 1600 and 2000 m along the ecotone between alpine meadows with dwarf shrubs (*Vaccinium spp.*, *Rhododendron spp.*) and Larch (*Larix decidua* Mill.), Spruce (*Picea abies* L.), or Swiss stone pine (*Pinus cembra* L.). Land abandonment was recorded in the area, mainly caused by a decline in forestry and traditional farming, which peaked locally in 1960s-1970s (Regione Lombardia and ERSAF 2012). The increase in the forested area from 1955 to 2007 is estimated at around 150.000-200.000 ha, with more than 10000 ha of pastures and hay meadows invaded by shrubland (Regione Lombardia and ERSAF 2012).

3.2.2. *Presence data*

We collected georeferenced locations of displaying Black grouse in spring obtained during an extensive survey on that took place in the period 1982-1985 in the whole area (Scherini et al. 1989). Overall, 545 display locations were digitalized on a GIS (QuantumGIS 2.18, QGIS Development team 2017) from original paper maps at 1:25,000 scale (*Istituto Geografico Militare*, IGM). We do not use the word "lek" as more than 40% of males displayed alone, a feature that is associated with low densities (Höglund and Stohr 1997), which is common occurrence in the Alps (Zbinden and Salvioni 2003). 137 display sites were located in inner Alps and 408 in the outer Alps. Mean display site elevation was 1755 ± 260m (min 900 m, max 2370 m). Precision in georeferencing display site had three main sources of stochastic error; the first source derives from the ability of the observers to locate display sites correctly on the map; second, map scale was relatively small, which means that even correctly located display sites had an intrinsic uncertainty of ± 50-75 m considering the dot size with respect to map scale (~2-3 mm); third, digitalization was made by comparing the original IGM map with updated topographic map, thus introducing a further source of error in case of difficult identification of display sites location on the recent maps.

3.2.3. *Species distribution model*

As stated in the introduction, the goal of the study was to evaluate variations in Black grouse habitat suitability related to changes in land cover/land use. First, we developed a presence/absence SDM referred to the 1980s based on the abovementioned dataset of display sites, implemented with topographical and land cover information. Then, we predicted the actual habitat suitability by applying the model to the same set of predictors relative to 2016 and we overlaid the two output presence/absence maps to identify changes in habitat suitability. Finally, we related suitability changes to 1980 predictors with a logistic model and we evaluated changes in landscape layout by calculating landscape metrics on the estimated distributions relative to the two considered periods. Although other factors contribute in defining a species ecological niche, most notably climate, we chose not to include them in the model in order to relate the observed change to LULCC only.

Black grouse is an ecotonal species, whose optimal breeding habitat is characterized by a complex horizontal and vertical vegetation structure and composition (Signorell et al. 2010; Patthey et al. 2012), where none of the three layers (herbaceous, dwarf shurbs, tall shrubs or trees) covers more than 75%, in a patchy layout (Magnani 1988; CREN Rhône-Alpes 2009; Schweiger et al. 2012). Thus, only field surveys or detailed phytosociological maps are capable to identify correctly these peculiar requirements (Patthey et al. 2012; Schweiger et al. 2012; Braunisch et al. 2016). This is a shortcoming when modelling the species distribution at large scale, since phytosociological maps are hardly available for whole regions. Therefore, SDMs for Black grouse are usually developed with general land use/land cover maps which classify the territory according to main vegetation structure categories (Decout and Signer 2010; Braunisch et al. 2011; Zurell et al. 2012).

To overcome these constraints, we implemented the SDM by processing land cover in terms of continuous variables. First, we transformed the land cover maps from categorical to continuous by applying a focal function which estimated the proportion of land covered by each class within the moving window. Then, we further integrated land cover information with a landscape eveness metric and a vegetation index obtained from remote sensing aimed at summarising vegetation density. Hereafter we are going to detail data and methods used in the SDM.

3.2.3.1. Land cover data

Lombardy has developed a land cover/land use map (*Destinazione d'Uso dei Suoli Agricoli e Forestali,* 'Use Categories of Agricultural and Forest Soils', hereinafter DUSAF map) that is periodically updated from photointerpretation. The classification used in DUSAF is in compliance with the hierarchical European nomenclature system of the CORINE Land Cover project, and has further regional-specific classes up to the 5th hierarchical level aimed at classify specific features of Lombardy landscape. The detail level is equal to a spatial resolution comparable with an 1:10000 printed map (i.e. minimum dimensional threshold of representability corresponds to 0.16 ha, smallest linear dimension of the polygon is 20 m). Information on current land cover was provided by the latest DUSAF map (DUSAF 5.0, issued in 2017), while past land cover was derived from a 1980 map (hereinafter '1980 map') whose legend was harmonized with DUSAF legend criteria up to the 4th hierarchical level. Since scale map resolution was coarser than DUSAF (1:50,000, minimum dimensional threshold of representability 4 ha), the map was densified using the first DUSAF version

(DUSAF 1.1, issued in 1999) and a land cover map derived from orthophotos taken in 1955. Both maps were eventually reclassified in 5 classes according to the species' eco-ethology, focusing on vegetation structure rather than composition ('high and medium density forest', 'low density forest', 'shrubland', 'meadows and pastures', 'unsuitable'). The class 'unsuitable' was subsequently discarded from the analysis.

3.2.3.2. Remote sensing data

As stated before, Black grouse requires a complex habitat composed by different land cover classes. This represents a limitation when SDMs are implemented for the species, since several land cover predictors should be considered simultaneously to identify correctly the species' requirements. Thus, we followed a remote sensing approach based on LANDSAT imagery to develop a vegetation density index which summarizes the optimal vegetation density for the species. LANDSAT is the longest-lasting remote sensing project, thus it suited our need to compare land cover at long term.

In mountain areas, ranges can significantly change surface reflectance by shading, which usually mixes with the spectral information used to distinguish land cover classes. In order to minimize this bias we derived the vegetation density index from bands ratio, an approach that normalizes spectral information by removing contrasts in light conditions and emphasizing radiometric data content (Gomarasca 2004; Campbell and Wynne 2011). The index was calculated from normalized short wave infrared bands (SWIR1 and SWIR2) ratio as SWIR1-SWIR2/SWIR1+SWIR2. This index in literature is known as NDTI (Normalized Difference Tillage Index, van Deventer et al. 1997), which was originally developed in the field of agricultural studies (Daughtry et al. 2006). NDTI was calculated from both reference periods from LANDSAT images (path/row: 193/28 and 194/28) with low cloud cover within the study area (<20%) selected from the vegetative period peak (early 1980s: LANDSAT 5, TM sensor, September 1984; present: LANDSAT 8, OLI sensor, July-August 2016). In the area of overlap between tiles a mean value was calculated. NDTI accuracy in distinguishing between different vegetation classes was tested with ground truthing surveys targeted at identifying training fields with uniform land cover. 26 training fields were surveyed in July 2016 in a study area located on the northern slope of Orobie Alps (Val Belviso, 46°05'30" N, 10°07'55" E). Each training field (> 1 ha) was assigned to 7 vegetation classes characterized by decreasing densities ('dense wood', 'sparse wood', 'wooded shrubland', 'shrubland', 'wooded meadows', 'shrubby meadows',

'meadows'). For each vegetation class the mean number of testing pixels was 49 (min 29, max 83). Pixel size matched the LANDSAT resolution (30m). LANDSAT images were processed with *raster* package (Hijmans 2016) in R 3.4.0 (R Core Team 2017).

3.2.3.3. Topographic data

Topographical variables were obtained from regional Digital Terrain Model (DTM) issued in 2015. Native resolution of the DTM was 5 m. Resolution was subsequently coarsed and the the raster aligned to LANDSAT grid (30m) using a bilinear interpolation, using *raster* package (Hijmans 2016) in R 3.4.0 (R Core Team 2017). To model Black grouse presence we included in the model, as terrain variables, elevation, aspect, slope and roughness (expressed as the difference between the maximum and the minimum elevation within a 3x3-cell window).

3.2.3.4. Environmental predictors

Three different proxies for land cover were used: DUSAF land cover reclassified classes, NDTI index and Simpson's Evenness Index (SIEI), which is a landscape index that expresses land cover diversity such that an even distribution of area among patch types results in maximum evenness (McGarigal and Ene 2015). Evenness is the counterpart of landscape dominance (i.e., evenness = 1 – dominance) already used in ecological investigations (Honnay et al. 2003; Schipper et al. 2011) and it is computed similarly to Simpson's Diversity Index (SIDI), which was shown to be positively correlated to Black grouse presence (Braunisch et al. 2016). SIEI was calculated from reclassified 4-class 1980 map and DUSAF 5.0 using FRAGSTATS 4.2 (McGarigal and Ene 2015).

In order model Black grouse distribution by means of continuous variables, we summarised land cover categories from DUSAF map to a 1000m- wide moving window, which is equivalent to 78 ha, corresponding roughly to the minimum species' home range on the Alps (Bernard-Laurent et al. 1998). This window size was a compromise between representativeness of breeding habitat and the risk of including unsuitable areas in case of larger windows sizes (i.e., valley bottoms, urban areas, glaciers etc.), especially when the elevational gradient was high. This approach also allows to account variables at the scale to which individuals perceive the environment (Graf et al. 2006) and helps reducing the effect of stochastic error in the georeferentiation of display sites locations. Hence, we applied this method also to native continuous variables, except elevation, aspect and slope. A focal median function was applied to continuous predictors' raster layers, while for categorical variables (land cover classes) we calculated the percentage of each class within the window.

All variables were resampled to match LANDSAT resolution (30m). Prior to model implementation, we performed a pairwise Pearson's correlation between predictors to ascertain that variables were not correlated (using r<0.70 as threshold). Predictors layers were elaborated with *raster* package (Hijmans 2016) in R 3.4.0 (R Core Team 2017).

Table 3.1 *- Predictors used for modelling Black grouse distribution.*

TYPE	SOURCE	NAME	VARIABLE	DESCRIPTION	UNIT
Land cover	**Land use map 1980 / DUSAF 5.0**	**FOR_HD**	High and medium density forest cover	proportion in a 1000m-wide circular moving window	%
		FOR_LD	Low density forest cover	proportion in a 1000m-wide circular moving window	%
		SHRUBS	Shrub cover	proportion in a 1000m-wide circular moving window	%
		MEADOWS	Meadows and pastures cover	proportion in a 1000m-wide circular moving window	%
		SIEI	SIEI index (derived from FOR_HD, FOR_LD, SHRUBS, MEADOWS)	median value in 1000m-wide circular moving window (focal)	unitless (range 0/+1)
	LANDSAT	**NDTI**	NDTI	median value in 1000m-wide circular moving window (focal)	unitless (range -1/+1)
Topography	**DTM (5 m resolution, resampled at 30m)**	**ELEV**	Elevation	cell value at lek location	m
		ASP	Aspect	cell value at lek location	degrees
		SLP	Slope	cell value at lek location	degrees
		ROUGH	Roughness	median value in 1000m-wide circular moving window (focal)	m

3.2.3.5. Statistical approach

In order to compare habitat suitability in the two considered periods, we built a past Black grouse potential distribution model using lek locations as presence data and environmental predictors related to the early 1980s, and subsequently we predicted current potential distribution providing the model with the actual variable layers. Given that only presence data were available, we used MaxEnt (Phillips et al. 2006; Elith et al. 2011), a machine learning approach based on the principle of maximum entropy, implemented in the package *dismo* (Hijmans et al. 2017) in R 3.4.0 (R Core Team 2017). Among niche modelling techniques, MaxEnt is the least sensitive to sample size

(Pearson et al. 2007; Wisz et al. 2008) and it employs a smoothing algorithm ('regularization') to avoid overfitting. A crucial aspect of MaxEnt modelling is the generation of background points ('pseudo-absences'), which could largely affect results (VanDerWal et al. 2009). Presences were unevenly distributed both vertically (elevation) and horizontally (among different areas within Lombardy) (Kramer-Schadt et al. 2013). We addressed the first issue by generating background points only within the elevational belt where the species lives in the region (1000-2600 m) to enhance model performance (Phillips 2008; Acevedo et al. 2012). Then, we mimicked a raster bias map provided to MaxEnt by creating an ad-hoc background layer, calculating first a bias map derived from the geographic density of presence points and, successively, generating 10-fold background points with the same density of presence points (Fourcade et al. 2014; Morganti et al. 2017). MaxEnt was run using default settings (Merow et al. 2013), which implies that all features classes (linear, quadratic, threshold, hinge, categorical) were used, according to the sample size (> 80 points). In order to cross-validate model, we followed the approach of Radosavljevic and Anderson (2014), according to which prediction results from k-fold model averaging. For each fold, the presence points sample gets randomly partitioned in a training set from which the model is built and a test set used to evaluate model performance. In our study, we chose k=5, with a training set/test set ratio equal to 80/20%. Performance statistics resulted from averaging AUC (Area Under Curve) k-fold model values. With the aim of obtaining a binary maps of potential Black grouse presence-absence and compare it between the two considered periods, we reclassified as 'suitable' only output values above the 'maximum training sensitivity plus specificity' threshold, which is the most conservative among the ones that are routinely computed by MaxEnt, considering as 'not suitable' values below the threshold (Liu et al. 2013). Finally, the predicted models were refined by discarding areas were model extrapolation occurred. This was achieved by producing a MESS (Multivariate environmental similarity surface) map, which measures the similarity of any given point to a reference set of points, with respect to the chosen predictor variables. Model predictions were masked by the MESS map by deleting cells in which it indicated extrapolation (values below zero). A final comparison map was eventually created with map algebra (cells suitable in 1980 and 2016, cells suitable in 1980 but not in 2016, cells suitable in 2016 but not in 1980). To compare the effectiveness of individual land cover data source in predicting Black grouse habitat (i.e. 1980 map classes, SIEI and NDTI), along with the “full” model we implemented 3 sub-models, discarding two data sources each time and eventually comparing AUC values.

3.2.3.6. Logistic model

In order to locate areas where habitat suitability reduction was likely to have occurred based on individual/predictor values, we fitted a logistic model on the comparison map raster cells. For each cell we extracted the value of each 1980 predictor, using them as independent variables, while as dependent variable we used a binomial unchanged suitability/lost suitability (coded as 0/1) response. Sample size (number of cells) was ~ 150000. Model was performed in R with *stats* package (R Core Team 2017).

3.2.3.7. Landscape metrics

Model outputs were eventually analysed in the light of changes of Black grouse potential distribution at landscape level, focusing on spatial patterns of suitable patches. In fact, habitat spatial structure is a crucial feature of species’ ecological processes (immigration/emigration, predation, density-dependent effects etc.) (Fahrig 2003) which may be compromised by a disruption in landscape patterns eventually affecting population persistence (With and Crist 1995). For each study period we computed landscape metrics using FRAGSTATS 4.2 (McGarigal and Ene 2015). FRAGSTATS implements landscape metrics at 3 levels (patch, class and landscape). As we dealt with binomial (presence/absence) output maps, we analysed them by means of class metrics, eventually retaining information on ‘presence’ class only. In **Table 3.2** we describe the computed metrics. All metrics were computed at two spatial scales, that is, for the whole study area and, separately, for inner and outer Alps. Metric values were then compared between periods and Alpine zone. To compute TCA (‘total core area’) we applied a 100 m edge depth (Temple 1986).

Table 3.2*– Landscape metrics calculated with FRAGSTATS.*

ACRONYM	NAME	DESCRIPTION	UNIT	PARAMETERS
AREA_MN	Area patch size (mean)	mean suitable habitat patch size	ha	
TCA	Total core area	total core area of suitable habitat	ha	edge depth = 100m
ENN_MN	Euclidean nearest neighbor distance (mean)	mean shortest straight-line distance between a focal patch and its nearest neighbor of the same class	m	
MESH	Effective mesh size	size of the patch that can be accessed from a random cell without leaving the patch; in other words, the area-weighted mean patch size.	ha	

3.3 Results

3.3.1. Species distribution model

Black grouse display locations were predicted with good accuracy (AUC=0.814), with a mean AUC over 5 cross-validation replicates of 0.787 (SD: 0.037), which can be considered a satisfactory performance given that climatic data were not employed. Elevation alone explained more than 40% of the model, followed by the proportion of dense forest and slope (**Figure 3.2**). Species' presence response with respect to individual environmental predictors was, approximately, linear or unimodal (**Figure 3.3**). Land cover classes predictors all showed a quadratic response as expected, with class coverage optima for dense forest, sparse forest, shrubs and meadows in the range, respectively, of 10-30%, 10-20%, 65-80% and 20-40%, which confirms the importance of structural vegetation heterogeneity. Consistently, Black grouse response towards SIEI was almost linear and positive, peaking at values close to 1.00, which identifies the maximum evenness of classes coverage. Low contribution of sparse forest in the model may derive by the scarce presence of this class within the study area. Likely, this is a photointepretation artefact included in the 1980 map deriving from failure to classify this diffuse vegetation structural typology. It is worth noticing the apparent bimodal response with respect to NDTI, which seems partly to contradict the response towards other land cover predictors. A likely explanation of this result may lie in the partial cloud cover of the 1980 LANDSAT images, which diminished the predicted NDTI values in overlapping areas between tiles, where a mean value was calculated, hence altering the species' response, as identified by the first peak between NDTI values ranging from 0.20 and 0.25. Terrain predictors contribution to the model ranged from high (elevation) to almost null (aspect). An expected elevation optimum between 1800 and 2000 m asl was seen; moreover, a preference for moderate slopes and a certain degree of slope roughness emerged.

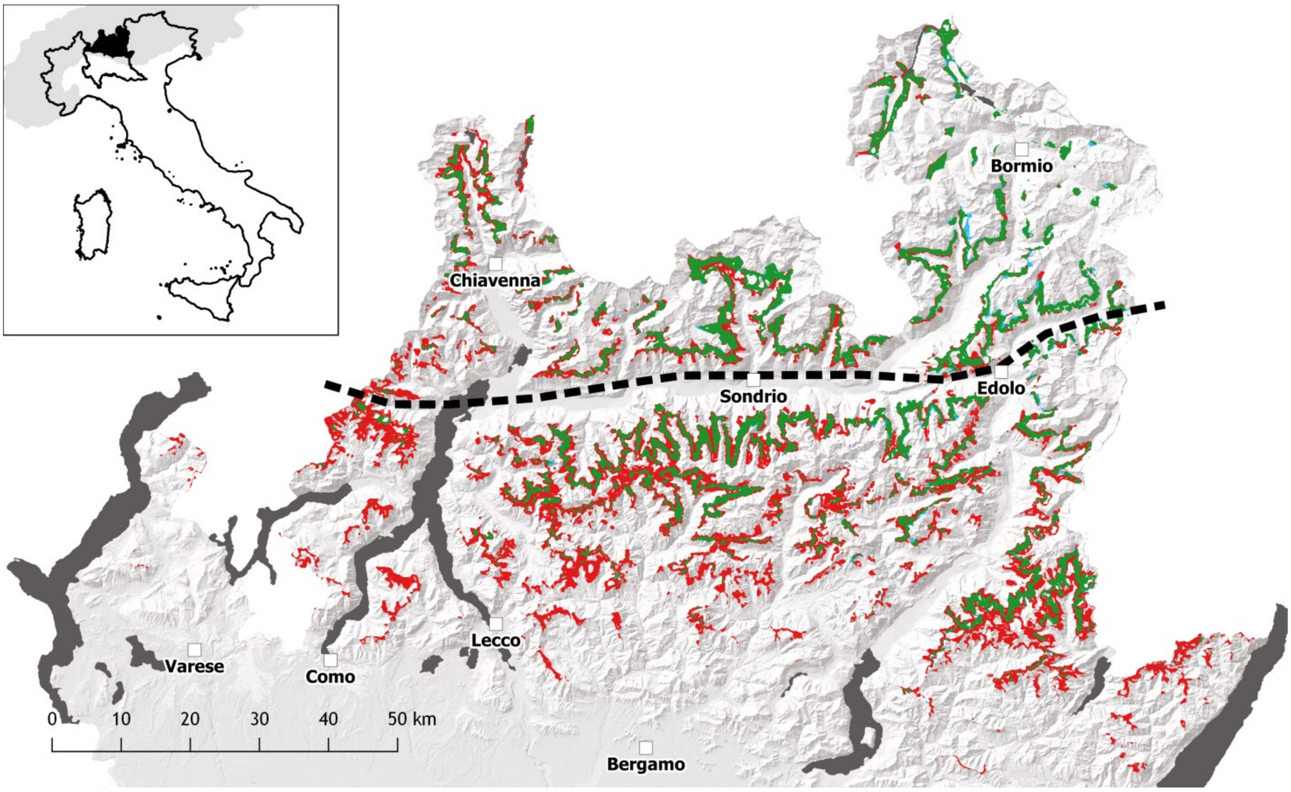


***Figure 3.1** – Comparison map between Black grouse predicted distribution in 1980 and 2016. Green: unchanged distribution; red: distribution in 1980 lost in 2016; light blue (barely visible): distribution in 2016 not predicted in 1980. Black line represents the Insubric Line. Inset: location of the study area with respect to Lombardy and Italy. Gray: the Alpine area.*

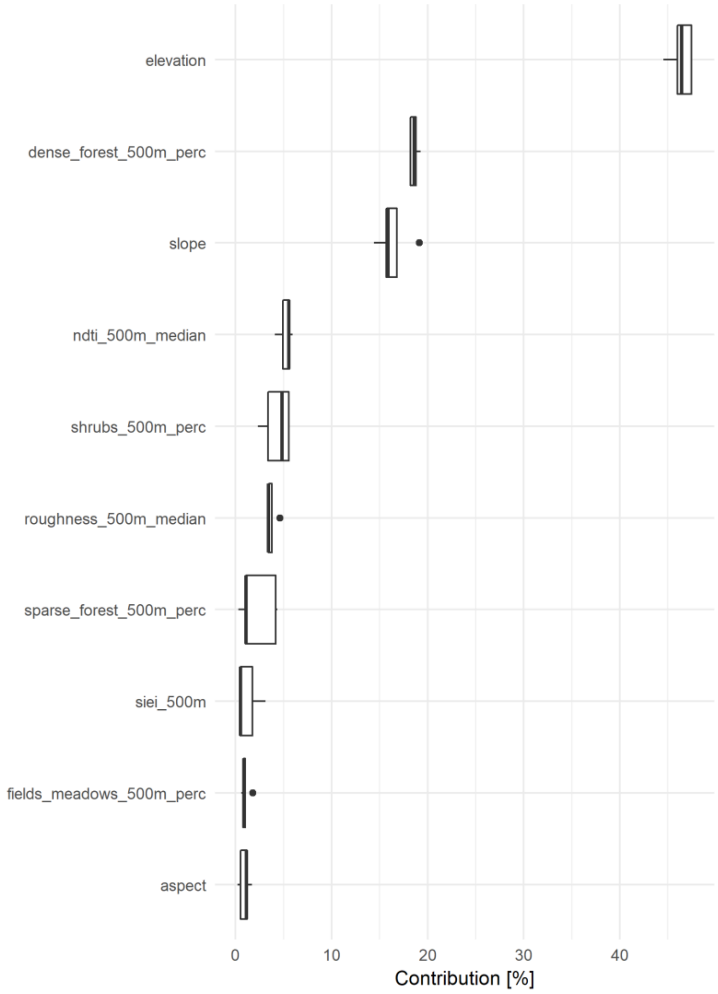


Figure 3.2 - *Estimates of relative contributions of the environmental variables to the model (median and 25-75% interquartile range of 5 model iterations)*

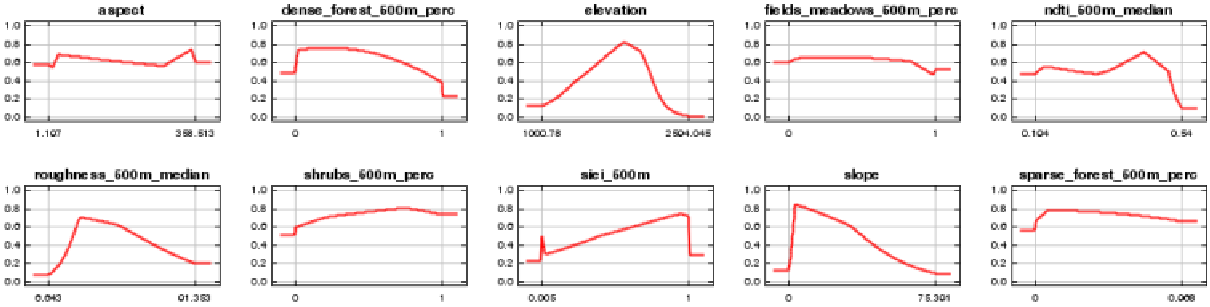


Figure 3.3 – *Predictor response curves as calculated by MaxEnt model*

3.3.2. Model comparison

Despite the bias introduced by cloud cover, NDTI-based sub-model accuracy was only slightly lower than 1980 map-based sub-model. In fact, for the 1980 map-based sub-model the AUC was 0.822, while for the NDTI-based was 0.792. SIEI-based sub-model was less accurate, with an AUC= 0.771. It must be noted however that 1980 map-based sub-model was implemented with 4 land cover predictors (dense forest, sparse forest, shrubs and meadows) while the remainders had only NDTI or SIEI as land cover variable.

3.3.3. Black grouse habitat suitability change

From the comparison map between suitable Black grouse distribution in 1980 and 2016, a diffuse and massive reduction in the study area emerged as result of land cover changes (**Figure 3.1**). At regional scale, habitat suitability shrunk from an estimated 137848 to 65143 ha, corresponding to a 52.7% reduction. Local gain in habitat suitability occurred, but to a negligible extent at regional scale (2729 ha), and limited to the eastern inner Alps, mostly at higher elevations with respect to 1980. Habitat loss occurred in inner and outer Alps unevenly. Indeed, in the inner Alps the reduction was moderate (-23.8%) with respect to the outer Alps (-66.1%), where the model predicted an almost complete habitat suitability loss in the pre-Alpine foothills. Overall, the large subalpine belt which formerly constituted a continuous suitable patch encircling higher ridges appears now fragmented in several patches. This is confirmed by the landscape fragmentation analysis implemented in FRAGSTATS, which showed a sharp reduction in the mesh size (MESH), which roughly corresponds to the area-weighted mean patch area (**Figure 3.4**), from 1022 to 72 ha. Consequently, the mean Euclidean distance between patches (ENN_MN) increased regionally from 218 to 336 m, and the mean patch area (AREA_MN) decreased from 129.8 to 96.5 ha, albeit marginally in the inner Alps (176.0 to 160.8 ha) and more substantially in the outer Alps (117.7 to 67.9 ha). This latter change involves a collapse of habitat ecological functionality, as habitat core-areas size (TCA), which correspond to areas where detrimental edge effects are likely not to occur, dropped to 40% of the original extent, and further down to 29% in the outer Alps. The logistic model confirmed the results emerging from landscape fragmentation analysis. Elevation accounted for the 70% of the explained deviance (**Table 3.1**). Habitat loss resulted more likely to have occurred at low elevations; more in details ,the model did not predict any stable habitat (i.e. unchanged between 1980 and 2016) below 1400 m, neither in inner nor outer Alps (**Figure 3.5**). However, habitat loss occurred at higher elevations in outer Alps with respect to inner Alps, In fact, the elevation at which probability of habitat loss dropped below 50% was 150 m higher in outer Alps (respectively, 1880 m and 1725 m) (**Figure 3.6**). Slope and aspect had minor effect on habitat change prediction, while roughness seemed positively correlated with habitat loss in the inner Alps (**Figure 3.6**). Looking at land cover, habitat change showed an opposite relation to dense forest and meadows; indeed, consistently with a forest ingrowth scenario, habitat loss was observed more often at low forest cover and high meadow cover values (**Figure 3.6**). The correlation of shrub cover is less clear; in the outer Alps no correlation emerged, while in the inner Alps the relation is similar to meadows, thus habitat loss is associated to higher levels of shrub cover. Habitat loss is oppositely associated to SIEI and NDTI, which represent land cover condensed indices, being negatively related to the former and positively to the latter. Thus, low vegetation structural evenness is positively associated with decreased suitability and, overall, has the third share of explained model deviance after elevation and dense forest cover, while NDTI showed a positive relation to increasing vegetation densities.

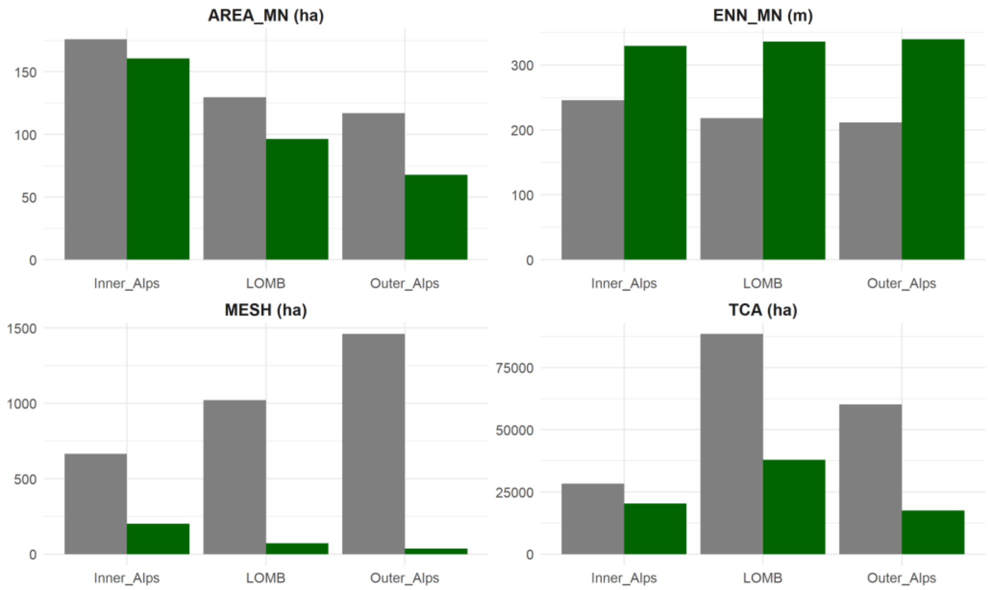


***Figure 3.4** - Comparison of landscape metrics in 1980 (gray) and 2016 (green) at regional level and separated between inner and outer Alps.*

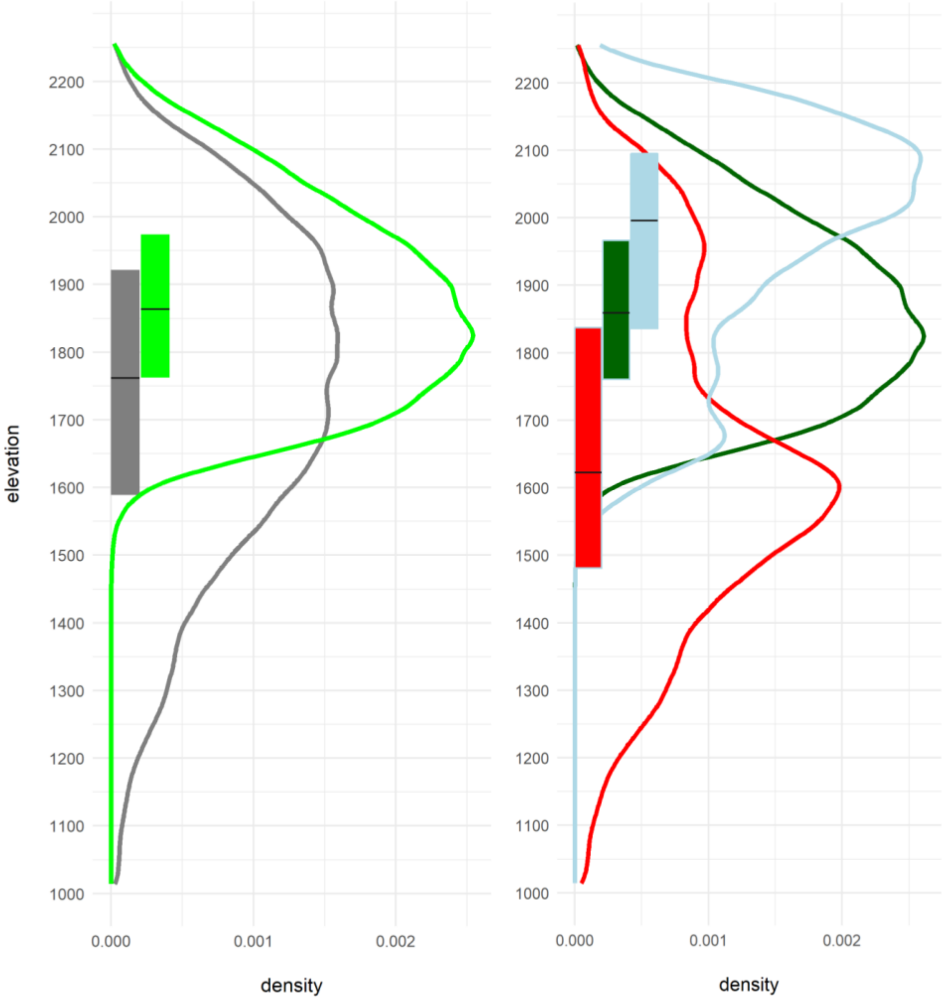


Figure 3.5 – *Habitat suitability changes in relation to elevation. Left: elevational distribution of Black grouse predicted habitat in 1980 (gray) and 2016 (light green). Right: elevational distribution of lost habitat (red), unchanged habitat (dark green) and gained habitat (light blue). Boxplots show median and interquartile 25-75% range.*

Table 3.3 – *Logistic model predicting habitat kss (cells that turned from suitable to unsuitable from the 1980s to current time) and predictor contribution in the explained deviance.*

	Deviance	**Resid. dev**	**% expl. dev**	**Pr(>Chi)**
elevation	493925.6		70.20	< 0.001***
dense_forest_500m_perc	80802.3		11.48	< 0.001***
siei_500m	66924.4		9.51	< 0.001***
roughness_500m_median	18990.6		2.70	< 0.001***
fields_meadows_500m_perc	15235.8		2.17	< 0.001***
ndti_500m_median	10702.9		1.52	< 0.001***
aspect	7654.2		1.09	< 0.001***
sparse_forest_500m_perc	5684.7		0.81	< 0.001***
shrubs_500m_perc	3041.7		0.43	< 0.001***
zone	375.4		0.05	< 0.001***
slope	252.4		0.04	< 0.001***
FULL MODEL	*703590.0*			
NULL MODEL		*2090908.0*		

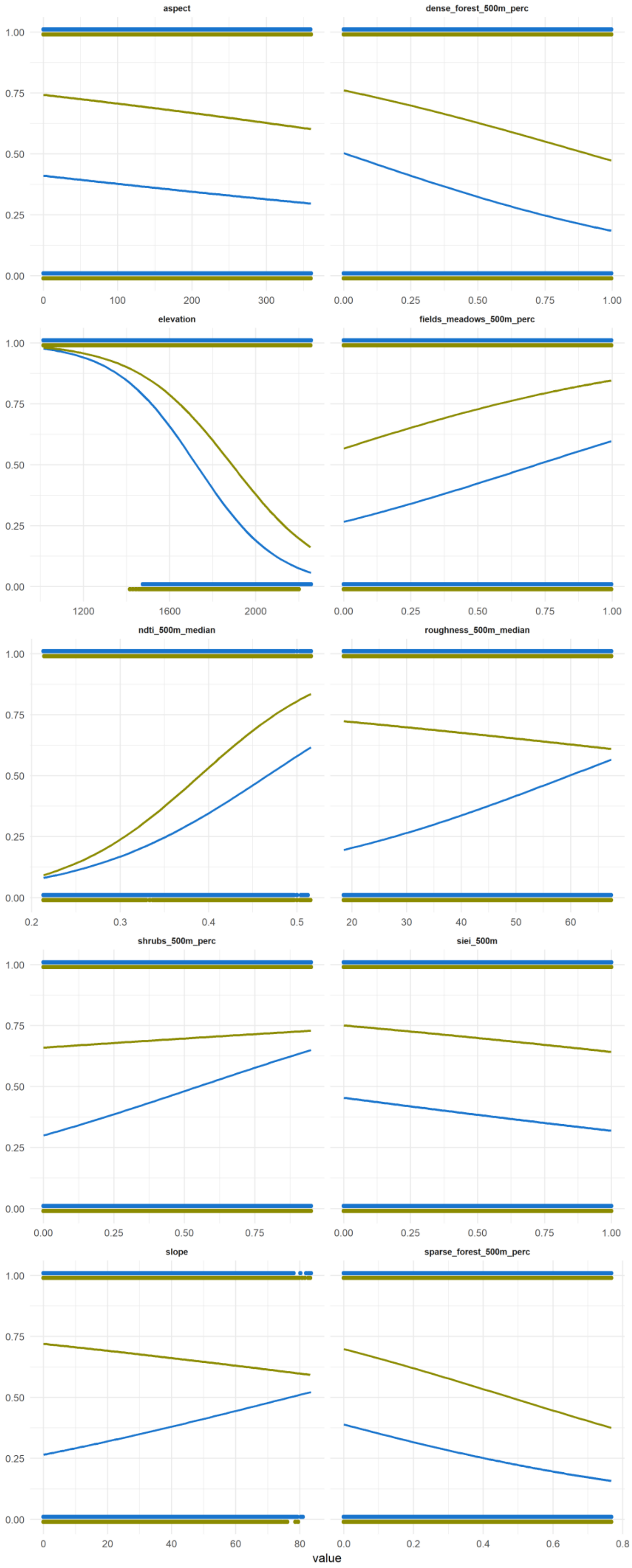


Figure 3.6 - *Probability of habitat suitability loss with respect to individual predictors (0 = suitable both in 1980 and 2016; 1 = suitable in 1980 but not in 2016)*

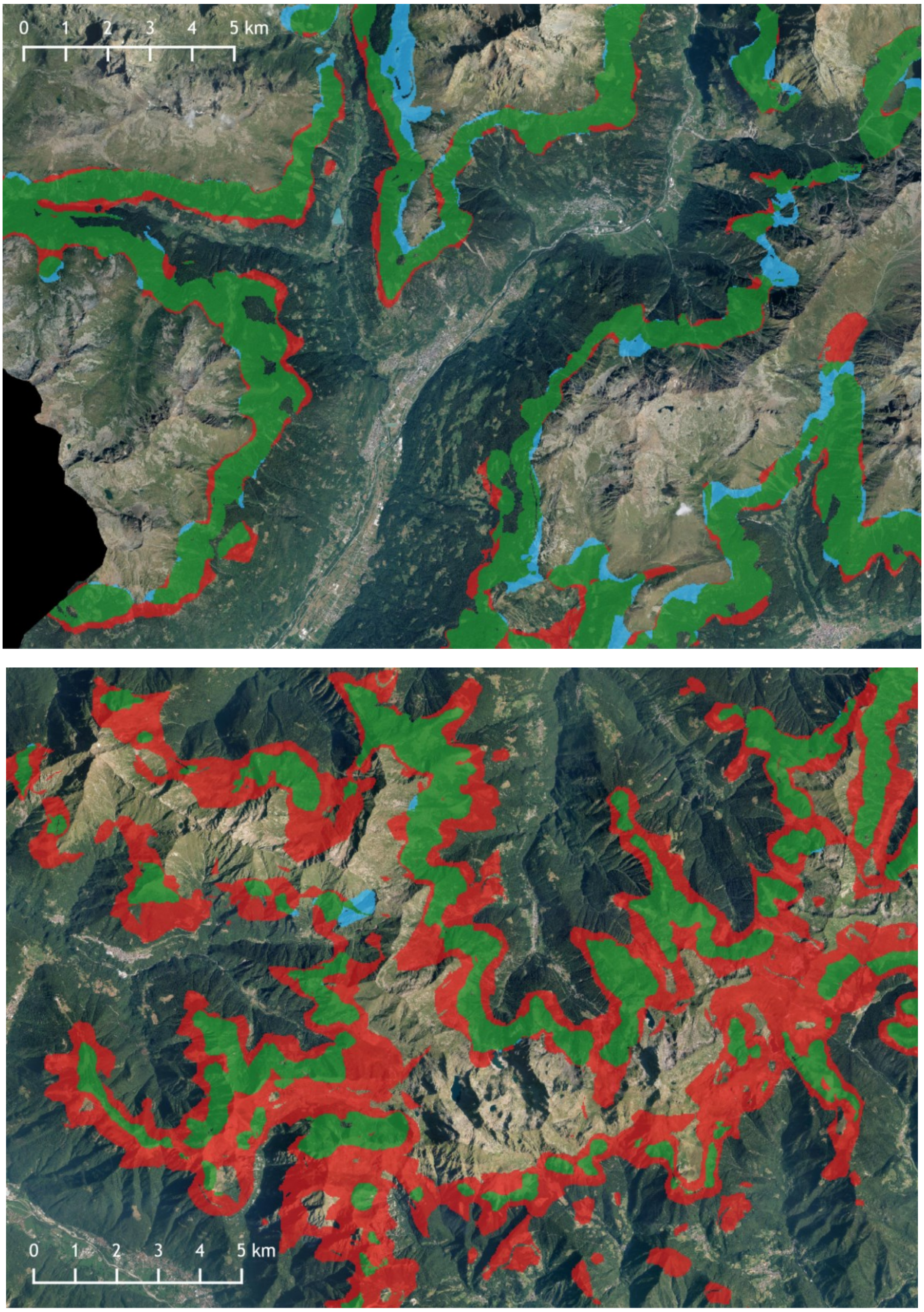


Figure 3.7 – *Different change of habitat suitability between inner and outer Alps. Top: inner Alps; bottom: outer Alps. Colours coded as Figure*

3.4 Discussion

3.4.1. Changes in Black grouse habitat suitability

3.4.1.1. Changes in elevation

A considerable environmental change has been occurring in subalpine ecotones in Central Italian Alps, which is likely to severly affect Black grouse conservation. Our study showed a substantial habitat suitability reduction and functional disruption related to land cover changes that have been occurring in the past four decades. We underline however that the model did not take into account several other environmental factors that contribute to define the species distribution, most notably climate, predation, availability of food plants and human disturbance. Hence, the model output might not be fully representative of the actual species distribution. In fact, in some of the predicted extinction areas the species is still present, although with small populations that markedly decline over the last decades (Martinoli, unpublished data). Most results that emerged from the analyses are consistent with a scenario of vegetation densification. Suitable habitat in 1980 was predicted to be distributed in a wider elevational range with respect to 2016 (interquartile range, respectively, 332 and 211 m) and median elevation shifted upwards by 101 m (1762 to 1863 m) (**Figure 3.5**). It must be noted that a large part of the observed elevational shift should be attributed to habitat losses at the trailing edge of the distribution rather than a genuine upward distribution shift. This explains the net overall suitable habitat reduction, which was almost halved in 35 years, since losses at low elevations have not been compensated by equal suitable areas gained at higher elevations. In this sense, habitat shrinking is likely a result of gap filling process of woody vegetations into former managed areas, given that the speed with which such dwarf shrubs develop depends primarily on elevation, with lower elevations (1600-1900 m) characterized by higher invasion rates (Tasser and Tappeiner 2002).

However, the estimated 100 m elevational shift is consistent with the 120 m upwards lek displacement observed by Marti et al. (2016) in an area of Central Switzerland from the 1970s to 2016, with the most substantial shift recorded from the late 1980s on. A further raising has been predicted during the 21st century by climate change scenarios for the species, whose distribution in Switzerland is expected to climb on average more than 400 m by 2100 (Zurell et al. 2012). A similar effect has been observed for the Rock ptarmigan, an Alpine grouse considered among the birds most threatened by climate change and treeline raising (Revermann et al. 2012; Imperio et al. 2013; Maggini et al. 2014; Ferrarini et al. 2017), which is predicted to undergo a notable shift of mean elevation of populations, possibly driven by population reductions or extinctions at the trailing edge (Desmet 2014; Pernollet et al. 2015).

3.4.1.2. Differential habitat loss in inner and outer Alps

Estimated habitat loss in Lombardy inner Alps was markedly lower than predictions for the outer Alps, where the extent of suitability reduction was 3-fold higher. As shown by **Figure** and **Figure** , these areas are mainly located on marginal ranges, characterized by lower elevations, by proximity to the Alpine foothills and by broadleaved treelines. According to De Franceschi (1994) the species' presence in these areas was a novelty of the 20th century, which followed a range expansion that occurred in the two decades after WWII ending. Black grouse settled in these areas thanks to the first phase of land abandonment, which coincides with an increase of habitat suitability owing to reduced human and cattle disturbance and transition of intensive hay meadows and pastures towards a semi-natural condition (Magnani 1992; Rotelli 2014). From the early 1980s we assisted to the second phase, where shrub encroachment eventually led to reduced suitability and finally local extinction of the "newly" settled populations.

The forestation rate in Lombardy from 1980 to 1999 was estimated in an impressive 4000 ha/year (estimated forested area in Lombardy in 1980 was ~500.000 ha), which later slowed down to 285 ha/year from 1999 to 2007 (Regione Lombardia and ERSAF 2012). This phenomenon in the outer Alps occurred much faster than in the inner Alps, favoured by warmer and wetter climate and mainly lead by broadleaved, faster growing species (Piussi and Pettenella 2000). In the outer Alps, traditional farming abandonment started in the 1950s, whereas in the inner Alps farming activities declined to a minor extent (Della Marianna et al. 2004). This differential change in farming pressure, together with the relative temporariness and instability of recent colonized areas in the outer Alps, which resulted from a transient situation between farming regimes, are likely to have determined the observed larger habitat loss south of the Insubric Line.

3.4.1.3. Habitats involved

Areas more likely to undergo suitability loss for Black grouse from 1980s to 2016 were mostly medium to dense forests or, on the opposite, clear grasslands located at low elevations (1500-1800 m) and, overall, characterized by low vegetation structural evenness. The proportion of cells that turned from suitable to unsuitable showed mostly a linear relation with respect to 1980 predictors, although Black grouse presence relation to vegetation layers cover has rather a quadratic effect, as it selects for mosaics where none of forest and low grasses cover more than 75% (Magnani 1988; CREN Rhône-Alpes 2009, this study). Hence, we hypotethise that habitat suitability loss occurred primarily in sub-optimal areas on the fringe of the distribution. If this hypothesis were true, the observed potential distribution reduction could have less severe negative impact on the species conservation than expected simply by considering the net habitat loss, as it affected areas characterized by marginal importance, which eventually became fully unsuitable. These areas mainly consisted of medium to dense subalpine larch (*Larix decidua* Mill.) and spruce (*Picea abies* (L.) H.Karst) forests close to the subalpine scrub belt, as evidenced by the relative high proportion of explained deviance of the logistic regression. However, it is likely that this category include also a certain proportion of one of the preferred habitat of Black grouse, that is, larch heliophilous woods with Ericaceae shrubs, which the photointepretation evidently failed to classify more correctly into the 'sparse forest' class, as stated before. This was confirmed by visual assessment on the field during fieldwork, when we visited sparse *Larici-Cembretum* woods known as being classified into the '3121' DUSAF category ('medium to dense conifer woods'). Sparse larch woods were historically kept open by so-called "wood pastures", mainly used in spring and fall before and after cattle was brought in pastures above treeline (Mayer et al. 2005; Garbarino et al. 2011). This traditional use of the forest affected the vegetation dynamics and structure favouring the conservation of patches of grasses and limiting shrub encroachment within forests (Mayer et al. 2005; Mayer and Stöckli 2005). Wood and shrub pastures suffered a -64% decline from 1955 to 2007 in Lombardy Alps, which currently cover just ~ 20000 ha (Regione Lombardia and ERSAF 2012). Hence, habitat loss may have occurred chiefly in abandoned wood pastures, where grass patches were soon invaded by *Rhododendron*. Recreation of the structural heterogeneity of wood pastures by selective cutting of dwarf shrubs is already one of the key features of habitat management to promote Black grouse (Magnani 1992; CREN Rhône-Alpes 2009; Rotelli

2014; Braunisch et al. 2016). Successful outcomes in terms of breeding success improvement have been shown after shrub re-opening interventions (Novoa et al. 2002; Rotelli 2014).

Encroachment into wood pastures could explain also the unexpected relation of habitat loss with respect to SIEI and NDTI, which apparently occurred more likely where habitat evenness was already low and vegetation density high. It is interesting to highlight that our study period coincide with the period when most of farm holding abandonment occurred in the Alps (an estimated 40% between 1980–2000, Tasser et al. 2007), causing primarily discontinuation of wood pastures and abandonment of larch meadows (Tasser and Tappeiner 2002). Surprisingly, slope had an almost negligible effect in determining habitat loss, although land abandonment was shown to be positively related to increasing slopes, since less accessible grasslands were the first where hay making and grazing discontinued (Gellrich et al. 2007; Bolliger et al. 2007; Camacho et al. 2008; Tasser et al. 2017). However, when only slope is considered, a strong relation between with habitat loss probability emerged for the inner Alps, while no effect was detected in the outer Alps. So, timing of abandonment may be the key to interpret the effect of slope; in outer Alps, where abandonment started well before than inner Alps, steep slopes were already encroached by shrubs in the early 1980s, while this process was still detectable in the analysed period for the inner Alps.

3.4.1.4. Habitat fragmentation

Even though high-quality habitat in the 1980s may have marginally lost suitability for Black grouse, at landscape level the study outlined deep habitat fragmentation. At medium-long term this could severely impact the species conservation. All elements of fragmentation were evidenced by the study: reduced mean patch size, mesh and core area, increased distance between patches. Most notably, mesh area (MESH) values sharply reduced, indicating that in the 1980s Black grouse could rely on a seamless strip-wise belt of suitable habitat which encircled the main ranges, which now appears as fragmented into multiple small patches. We hypotethise that high quality patches in 1980 were likely to be merged in a matrix of sub-optimal areas which represented a buffer zone towards unsuitable habitat less intensively used by the species, but still providing useful features of a secondary ecological niche (e.g. cover from predation, secondary roosting or feeding areas). These transition areas appear now as fully unsuitable. The mean patch area (AREA_MN) decreased to a lesser extent with respect to mesh area, suggesting that in the 1980s Black grouse habitat was spatially arranged at landscape scale into few very large patches representing the core of the species distribution, surrounded by a network of smaller patches on peripheral ranges. Currently this structure seems to have evolved into a more even arrangement of suitable patches resulting from breaking up of the former large patches, and the loss of peripheral patches. Albeit it increased by 35% during the considered period, mean distance between patches is however limited (335 ± 728 m, median is 134 m) and actually does not seem to represent a threat. From a landscape perspective, negative effects may derive from core-areas reduction, which dropped to 40% of the extent predicted in the early 1980s. This result, coupled with the loss of sub-optimal habitats, at medium-long term may threaten Black grouse conservation by enhancing edge effects, which expose individuals to associated ecological changes (Wilcove et al. 1986; Murcia 1995). Most notably, nest and brood predation by generalist mammal and bird predators was shown being proportional to the degree of landscape fragmentation in Fennocandian grouse populations (Andrén et al. 1985; Andrén 1994; Kurki and Lindén 1995; Storaas et al. 1999; Kurki et al. 2000), even though in these studies fragmentation was related to agricultural land interspersed in forest patches, which increases the detetion probability of nests by corvids. These results might not fully apply to our study, since in this case fragmentation is boosted by dense forest and corvids are not among Black grouse main predators in the Alps (Caizergues and Ellison 1997). These are open areas and sparse forest predators (Goshawk *Accipiter gentilis*, Golden eagle *Aquila chrysaetos*, Stoat *Mustela erminea*), dense forest predators (Stone marten *Martes foina*, Pine marten *Martes martes*) and, chiefly, the ubiquitous Fox *Vulpes vulpes*. Hence, the overall predation rate may not be influced, but rather we might expect a change in the prevalence of predators, with unknown consequences on population dynamics.

A ground-dwelling bird characterized by poor dispersal capabilities as the Black grouse (Caizergues and Ellison 2002) is likely to be more susceptible to habitat fragmentation with respect to other birds, which are capable to thrive also on a certain degree of fragmented landscape by connecting patches with flight (Andrén 1994; Schmiegelow et al. 1997). Alpine populations are already more exposed to population fragmentation by reason of the complex topography and the presence of high ridges that likely prevent bird displacements (Pierson et al., manuscript). As a result, gene flow is limited and evidences of genetic drift are seen (Caizergues et al. 2003b).

3.4.2. Use of remote sensing techniques

Remote sensing techniques are widely applied in the field of biodiversity monitoring and land cover changes (Khare and Ghosh 2016). One of the major shortcomings in land use/land cover changes studies is represented by the availability of past land cover information, which is often available at small scale only (agricultural/forest cadastre, aerial photography) and therefore unsuitable for larger scale analysis. Remote sensing techniques are powerful tools that overcome the problem and were already employed in the assessment of shrub encroachment in Black grouse habitat (Braunisch et al. 2016). However, the temporal scope of the analysis depends on the availability of past imagery. LANDSAT is the longest-lasting remote sensing project of the Earth and allows to stretch the temporal extent to the early 1980s. The use of remote sensing-derived NDTI as proxy for identifying Black grouse habitat was encouraging, even though that we could not avoid the use of images with partial cloud cover. To our knowledge is the first time that NDTI was employed to implement species distribution models of an animal species. NDTI-based models could then be applied to estimate changes in habitat suitability related to land use/land cover at wider spatial scale, such as the whole Alpine range, albeit ground truthing validations should be performed in other study area to fine-tune the response of the index to different phytosociologial associations.

Chapter 4

Alpine Rock ptarmigan (Lagopus muta helvetica *Thienemann) at range margins: evidence for low ecological plasticity*

ABSTRACT. In this Chapter we evaluated whether Rock ptarmigan populations living at range margins on the trailing edge of a predicted displacement induced by climate change can use habitat in a plastic way in order to adapt to suboptimal environmental conditions. Therefore, the aim was to test if in a climate change scenario the species hypotethised high vulnerability could be somehow lower than predicted. Using a small dataset of georeferenced locations, we compared the use of habitat in terms of topographic variables of two populations living in ecologically different areas of the Western Alps, one located in the core of the Alpine range and one in the southern edge of the distribution, 65 km from the sea. In such condition, plasticity would emerge as lack of selection of environmental features and a more even use of space. Contrary to the hypothesis, the use of habitat of Rock ptarmigan in the suboptimal area was markedly determined by elevation, which caused a lack of seasonal movements related to climatic constraints. Conversely, in the area located in the core of the Alps the use of habitat seems to be influenced by topography only marginally and ptarmigans likely exploits a wider range of habitat features. This results suggest that the species may not be able to buffer the negative effects of climate change at range margins and, therefore, these populations may go extinct sooner than expected.

KEYWORDS: plasticity, Alps, suboptimal habitat, Rock ptarmigan

4.1 Introduction

Recent increase in human pressure and global warming (Sala et al. 2000; Houghton and Intergovernmental Panel on Climate Change 2001) is reshaping species distribution and causing local extinctions, especially in species with narrow ecological niches (Moss et al. 2001; Thomas et al. 2004; Sekercioglu et al. 2008). A major paradigm of biogeography is 'centre-periphery' hypothesis, which states that at species range margins, where the limits of the distribution are constrained by environmental factors, individual fitness is generally lower than in the core of its distribution (Kawecki 2008), and, hence, marginal populations would be more prone to extinction than those from the centre (Lawton 1993). Effectiveness of such constraints on fitness depends, among other factors, on local adaptation of the populations, phenotypic plasticity, steepness of environmental gradients and gene flow (Kawecki 2008). These features are of particular importance at the distribution edge, especially when climatic changes occur (Davis and Shaw 2001).

Alpine Rock ptarmigan vulnerability to climate change has a manifold component. First, the species' ecological niche and, hence, distribution, is markedly constrained by climate, and, chiefly, by low summer temperatures (Revermann et al. 2012; Imperio et al. 2013). Second, the response to temperature (Marti and Bossert 1985; Revermann et al. 2012; Visinoni et al. 2014) and vegetation cover (Nelli et al. 2013) is narrow, preventing it from exploiting different conditions, unlike, for example, Rock partridge, which has a broader ecological niche only partly overlapping with Rock ptarmigan (Bernard-Laurent and De Franceschi 1994). Third, dispersal possibilities northwards are virtually impossible, unlike Scandinavian and North American populations (Brommer 2004; Huntley et al. 2007; Lenoir and Svenning 2015); thus, the species could only respond to a temperature increase by shifting distribution on the elevational gradient, which determines an inevitable range reduction and increased fragmentation (Pernollet et al. 2015). Fourth, it can be generally regarded as a marginal and isolated population with respect to the core of the global range. Thus it experiences the drawbacks already outlined in the thesis introduction, albeit the Alpine range is large enough to allow the identification of core and peripheral environmental conditions within it, even at small scale (Fasel and Zbinden 1983). All this considered, Alpine Rock ptarmigan conservation at medium term is regarded as severely threatened by climate change (Revermann et al. 2012).

However, in extreme habitat conditions species often make the best out of a non-optimal situation (Kawecki 2008). Indeed, populations living at range margins are often characterized by a greater plasticity with respect to populations living at the core of the distributions, or even show local genotypic adaptation. As a consequence, they are able to thrive in sub-optimal environmental conditions, if compared to the ones that core populations experience (Volis et al. 1998; Sunde et al. 2001; Otaki et al. 2010; Romeo et al. 2010). Nevertheless, plasticity and adaptation are rarely taken into account when modelling species' range shifts consequent to climate change, and an equal response across populations is generally assumed (Jetz et al. 2007). Valladares et al. (2014) have recently highlighted that range predictions in a global warming scenario could change substantially when differential plasticity between leading edge, core and trailing edge populations is accounted for, combining this feature with dispersal possibilities, which was already known to intensify or to buffer the actual response (Thomas et al. 2004). A possible higher plasticity of populations on the distribution trailing edge would mitigate the extinction risk. If this would apply to Rock ptarmigan, predicted negative effects of climate change for its conservation may be overestimated.

In order to test this hypothesis we performed a study to analyse habitat use of two Rock ptarmigan populations located in Western Italian Alps, one in the inner Alps with elevations rising up to 4000 m asl and one in the southern fringe of the Alpine arch, situated just 65 km from the Mediterranean sea. In particular, using a small dataset of GPS locations, we compared the selection for topographical features, considering elevation, slope and aspect, to investigate if the southern populations exhibit range margin plasticity which could buffer negative effects of climate change.

4.2 Materials and methods

4.2.1. Study area

The two study areas are both located in Piedmont region, 140 km distant from each other (**Figure**). The area in the inner Alps, hereinafter "PNGP" (800 ha), was inside the Gran Paradiso National Park, close to the border with Aosta Valley and France, nearby Nivolet lakes (45°28′01″ N, 7°09′31″ E). Elevation varies from 2100 to 3400 m asl. The marginal population lives in an area (1000 ha).at the top of Stura valley at the border with France (44°13′43″ N, 7°02′10″ E), hereinafter called “CACN4”. Elevation varies from 1900 to 2700 m asl. According to the Forestry Map of Piedmont Region (hereinafter FMPR) four land cover categories are present in the two areas: rocks and screes (PNGP 90%; CACN4 70%), rupicolous vegetation (PNGP 5%; CACN4 15%), high altitude grassland (PNGP 5%; CACN4 10%), Alpine shrubland (CACN4 5%). The species is protected in PNGP but hunted in CACN4.

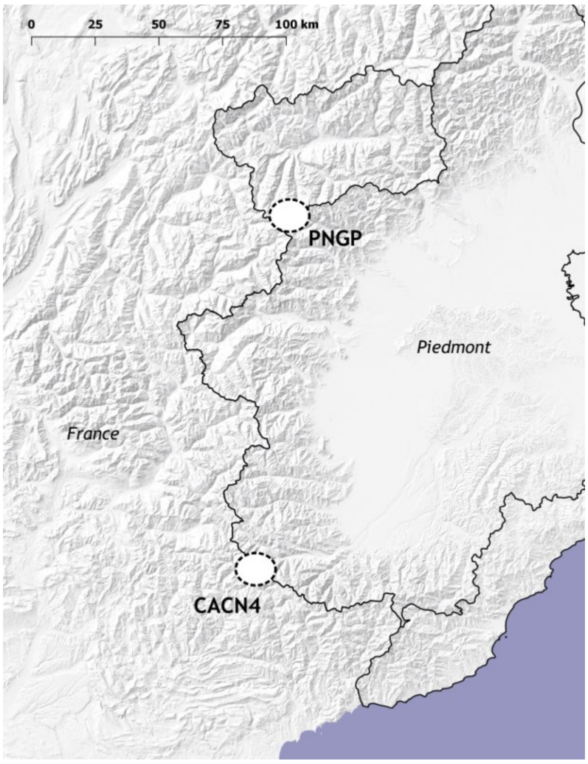


***Figure 4.1**– Locations of study areas*

4.2.2. Data collection

Ptarmigan surveys were carried out between May and October in 2010-2011 in PNGP, and in 2011 only in CACN4. Years 2010 and 2011 had different weather conditions: 2010 was characterized by a wet spring and hot summer, while 2011 had a dry spring and fresh summer. Birds were located using different methods in relation to the period of the breeding season. In May ptarmigans were located with the help of recorded cock calls. In June-July animals were located with the help of recorded juvenile calls. From August to October ptarmigans were located with pointing dogs, when possible

(80% of total locations) we recorded sex. Every location was recorded using a GPS, with a positioning precision between 3 and 10 m. Throughout the study period animals were located also by periodic active search in the study areas.

Data on elevation, aspect and slope were measured using a Digital Elevation Model (DEM, 50 m cell size). Land cover was classified according to FMPR categories. This map was developed from photointerpretation and field surveys performed in year 2000 (reference scale 1:25000, smallest mapping unit 1 ha).

4.2.3. Statistical analysis

Data of each area were pooled, after testing with an ANOVA that the chioce of topographic variables (elevation, aspect, slope) was not sex- or, in PNGP, year-biased. In fact, differential use of habitat between sexes (Favaron et al. 2006), which include female-biased dispersal (Martin and Hannon 1987; Warren and Baines 2002), or the uneven weather conditions (Marti and Bossert 1985; Scherini et al. 2003) could influence the spatial behaviour of Rock ptarmigan.

Comparison of the use of habitat between the study areas was tested with an ANOVA followed by post-hoc tests (Tukey's range test) to assess for effects of elevation and slope on ptarmigans locations. We evaluated the use of aspect, which has a non-uniform distribution, with a circular ANOVA (Mardia and Jupp 1999). Elevation and slope data met the assumptions of normality (Shapiro-Wilk test, $W > 0.90$). For aspect, non-uniform distribution of data was appropriately tested using Watson test. We performed also the same analysis for each area separately to test for significant monthly differences in the use of topographic variables, which usually characterise the spatial behaviour of the species (Scherini et al. 2003; Favaron et al. 2006; Pernollet et al. 2015).

Then, we compare habitat availability between the two areas testing for differences in frequency distribution (availability) of topographic values. A chi-square test was performed for each topographic variable considered after categorization of continuous variables (breaks every 100m for elevation, 10° for slope, 22.5° for aspect).

Finally, we tested for habitat selection of ptarmigans in the two areas. First, we computed Ivlev Electivity Index (Ivlev 1961) for each variable (elevation, slope, aspect and land cover) after categorization of continuous variables using the abovementioned criteria used for the chi-square test on habitat availability. Given the proportions of available and used habitat categories, a positive habitat selection is defined for index values in the range ≥0.5 – 1. Second, logistic regression was performed for each area separately in order to evaluate the effect of elevation, slope, aspect and land cover on ptarmigan locations (n=73). For this purpose we randomly generated a 10-fold number of pseudo-absences with respect to presences within the study areas . A final model was selected using a backward stepwise variable selection procedure excluding step by step from the complete model the factor that was least significant ($p > 0.05$) until only significant factors were left.

All analyses were performed using the R software 3.4.0 (R Core Team 2017), in particular using the functions provided by the *stats* and *circular* (Agostinelli and Lund 2017) packages.

4.3 Results

The frequency distribution of all the topographic variables resulted different between the two study areas (elevation: chi-square= 5653.2, df=15, $p<0.001$; slope: chi-square =840.7, df=6, $p<0.001$; aspect: chi-square=1769.6, df=15, $p<0.001$).

Overall, 73 locations were recorded: 51 at PNGP (19 in 2010, 32 in 2011) and 22 at CACN4. A first comparison between years at PNGP showed that there were no differences in altitude selection (average altitude in 2010 and 2011 respectively, 2882±509 m and 2824±509 m asl, ANOVA: $F_{1,49}$=3,67; P=0.06), choice of aspect (2010: 250±44 degree; 2011: 225±40 degree ; circular one-way ANOVA: $F_{1,50}$=0.91; P =0.35), or slope (2010: 14.7±2.9 degree: 2011: 13.1±2.4 degree, circular one-way ANOVA: $F_{1,49}$=0.29; P=0.60), therefore for successive analysis we pooled data of 2010 and 2011. Land cover categories use was not compared between years since all locations in PNGP lie in the same category (rocks and screes).

Next, we tested for difference between sexes in the selection of topographic variables for each area separately. There were no differences between males and females in selection of any of the topographic variables: elevations (ANOVA: PNGP $F_{1,50}$=0.57, P=0.46; CACN4 $F_{1,21}$=0.48, P=0.50), aspect (circular one-way ANOVA: PNGP $F_{1,50}$=0.23, P=0.64; CACN4 $F_{1,21}$=1.04, P=0.32) and slope (circular one-way ANOVA: PNGP $F_{1,50}$=0.05, P=0.83; CACN4 $F_{1,21}$=1.05, P=0.32). Based on these results, in successive analysis locations of both sexes were pooled.

Ptarmigan locations at PNGP study area were on average at higher elevations than at CACN4 (respectively 2845± 502 m and 2564±453 m asl; ANOVA: $F_{1,71}=97.6$; $P<0.01$). Monthly variation in elevations of locations was significant in PNGP (ANOVA: $F_{5,45}=6.26$; $P<0.01$), but not in CACN4 area (ANOVA: $F_{4,17}= 0.33$; $P=0.85$). At PNGP, birds were at lower elevations in May than in August-October (Tukey test: all $P<0.01$), and in July they used lower elevations than in August and September (Tukey test: $P< 0.05$).

Ptarmigan also selected different slopes between study areas (circular one-way ANOVA: $F_{1,71}=11.0$; $P<0.01$, Fig. 2; Fig 3): they preferred shallow slope at PNGP compared to CACN4 where there was a more uniform selection of different slopes. Likewise, aspect was not uniformly distributed (Watson $U^2=0.74$; $P<0.01$) and aspect selection differed between study areas (circular one-way ANOVA $F_{1,72}=21.9$; $P<0.01$).

A logistic regression model was calculated for each area, considering both topographic variables and land cover classes, and the stepwise procedure selected for the same variables in each area. Land cover variables were first removed and only topographic variables were selected in the final models, which in both areas resulted slope (PNGP; coeff. estimate= –0.075, z value=-4.635, p<0.001; CACN4, coeff. estimate= –0.060, z value=-2.574, p<0.01) and elevation (PNGP, coeff. estimate= 0.003, z value= 3.772, p<0.001; CACN4, coeff. estimate= 0.012, z value=4.215, p<0.001). However, the deviance explained by the model resulted remarkably higher in CACN4 (32.3%) with respect to PNGP, where elevation and slope were able to explain a mere 9.8% of the null deviance.

The effect of elevation on ptarmigan locations shown by the logistic regression is consistent with the results of the Ivlev Electivity Index in both areas (PNGP: 2901-3000 m, Ivlev index=0.52; CACN4: 2601-2700 m, Ivlev index=0.57). Conversely, no selection for specific slopes emerged from the analysis, as it did not for land cover categories. Easterly aspects were selected in CACN4 (45°-67.5°, Ivlev index=0.53; 135°-157.5°, Ivlev index=0.70), but not in PNGP.

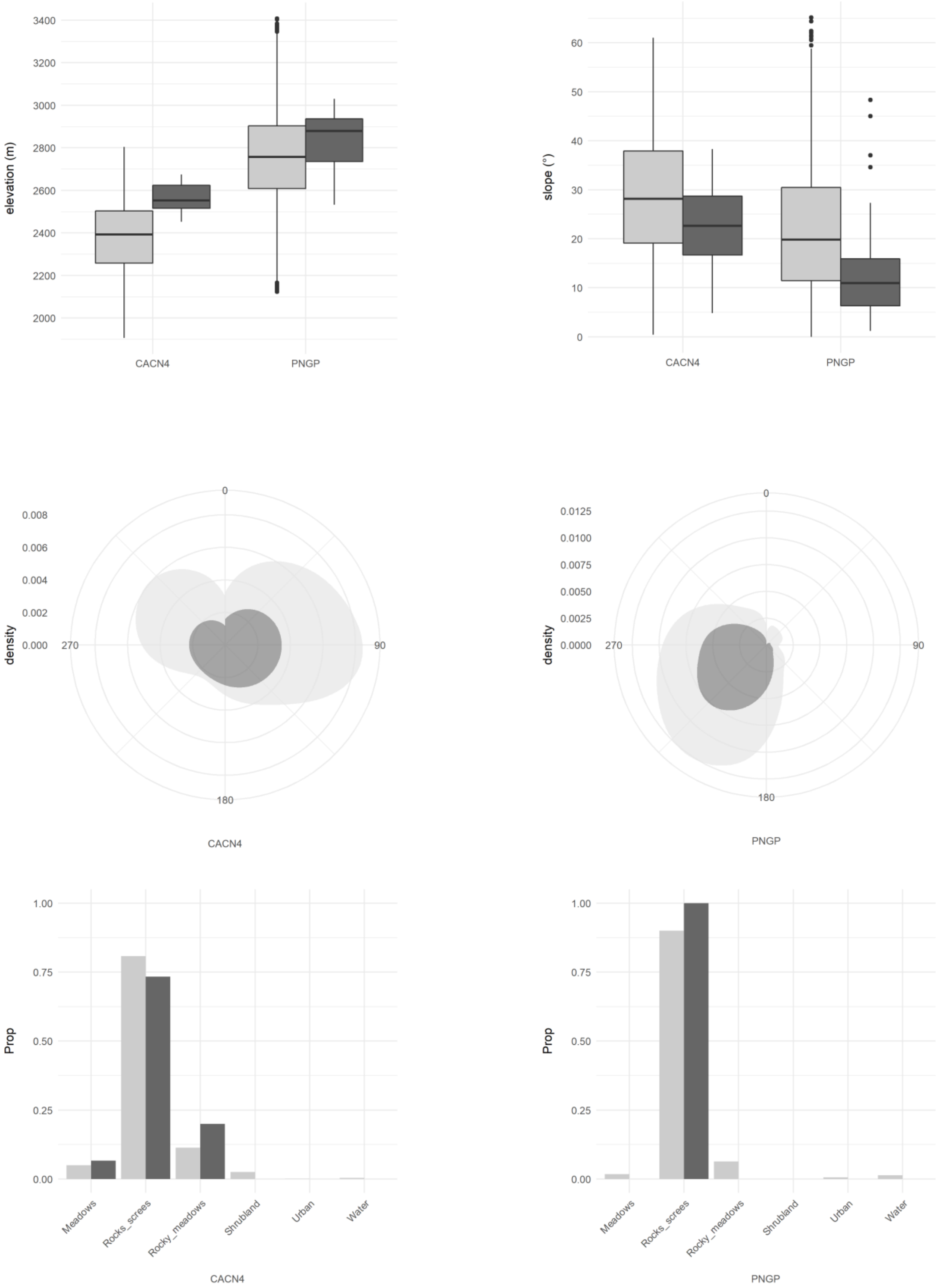


Figure 4.2 *– Comparison between habitat use and habitat availability in the two study areas with respect to topographical variables and land cover. Light gray refers to habitat availability and dark gray refers to habitat used by Rock ptarmigan. Top left: distribution of habitat availability and habitat use with respect to elevation (boxplot hinges indicate 25-75% interqurtile range). Top right, slope. Middle: density of available and used aspects within the study areas (left, CACN4; right, PNGP). Bottom: proportion of land cover categories (as defined by the Forest Map of Piedmont Region, FMPR) available and used in the study areas (left, CACN4; right, PNGP).*

4.4 Discussion

Albeit the two analysed populations live in different environments, the results of this study seems to reject the hypothesis that marginal Rock ptarmigan populations may exhibit a higher ecological plasticity with respect of populations living in optimal habitat conditions in the core of the distribution range. On the contrary, it may be true the opposite, since a wider plasticity emerged in PNGP while in CACN4 the species showed narrower selection for topographic features.

Topography in the two areas is different. PNGP is characterized by higher elevations and more gentle slopes, and, generally, it exhibits a broader availability of different topographic features, while the environment in CACN4 resulted much more constraining to Rock ptarmigan, with lower elevations that abruptly end below 2800m and steeper slopes, which are usually avoided by the species (Zohmann et al. 2013; Pedersen et al. 2013). In such conditions, plasticity would emerge as lack of selection of environmental features and a more even use of space.

Contrary to the hypothesis, the species seems to use the habitat in similar way in the two areas as far as topography is concerned. Elevation was the main factor affecting Rock ptarmigan habitat use in both study areas, as shown both by the logistic model and Ivlev Electivity Index. The effect of elevation is likely to be strongly correlated to temperature constraints, which prevent the species from exploiting areas at lower elevations, which would likely result too warm for the species physiology and ecology. This is consistent with studies that show that July temperature is a major factor shaping distribution, both at macro- and microscale (Revermann et al. 2012; Visinoni et al. 2014; Furrer et al. 2016). Besides higher elevations, the species positively selects gradual slopes in both areas. Gentle slopes are related to the presence of snow patches and nival vegetations, which represent important microhabitat features of the species habitat (Revermann et al. 2012; Pedersen et al. 2013). The avoidance of steep slopes was already shown by other studies that took topography into consideration in analysing the habitat of the Rock ptarmigan (Zohmann et al. 2013; Nelli et al. 2013).

In must be noted, however, that, overall, topography only marginally affected use of space in PNGP, since it explained less than 10% of observed variance, while this percentage amounts to almost 33% in CACN4. In other words, in PNGP other variables, such as vegetation, likely affect ptarmigan use of space, suggesting a higher plasticity than birds living in CACN4, where climatic constraints strongly determine habitat selection even if lower elevations are present within the area.

Therefore, according to the classification of plasticity intraspecific variation presented by Valladares et al. (2014), we speculate that Rock ptarmigan may not belong to the scenario 3 ('high margin plasticity'), but it should rather be assigned to scenario 4 ('high central plasticity'). If dispersal possibilities were practically non-existent, as they are actually given the lack of contiguous high mountain ranges north of the Alps, this would shift the species' response under climatic warming from a situation where range reduction would be rather even between core and marginal populations to a situation where severe range reduction would be observed chiefly in marginal populations, while core populations would result less affected. Evidently, in this latter case peripheral populations could not play an important role for the persistence of the species under climate change, as it would happen if they exhibited more ecological plasticity.

As stated before, this study is based on a small number of locations, which were likely the cause of some inconsistencies found (e.g. GLM and Ivlev index for aspect selection in CACN4). To confirm this results, the analyses should be repeated on a larger dataset and extended to climate and to fine-scaled land cover maps, since FMPR resolution proved to be too coarse to predict Rock ptarmigan habitat selection. Nelli et al. (2013) already used the FMPR for modelling Rock Ptarmigan cocks territories, although its predictive capability proved to be weaker than a phytosociological map due to insufficient spatial resolution. When phytosociolgical information is available, topographic variables became not significant in the models, consistently with the importance of the ecological features associated with vegetation cover for the individuals (food sources, predation avoidance, microclimate etc.). Unfortunately, no phytosociological map was available for either study areas, therefore FMPR provided the most detailed information available on land cover. Large scale or low resolution maps have limited predictive power to detect relevant habitat features of Rock ptamirgan (Revermann et al. 2012; Nelli et al. 2013). At the spatial scale of our study, in the order of magnitude of several territories, microhabitat features such as the presence of boulders (Rae 2015). the height or dwarf shrubs (Schweiger et al. 2012) or the presence of depressions and snowfields (Pedersen et al. 2013; Visinoni et al. 2014) become key features to describe accurately the species use of space. Nevertheless, topography provides still important information to model the species habitat preferences at territory scale (Revermann et al. 2012; Pedersen et al. 2013; Nelli et al. 2013).

Ptarmigan breeding success in the two areas are similar over the years (Bisi et al. 2012), which suggest that, currently, the population fitness may be not negatively influenced by marginality by living just below mountain ridges. In fact, marginal populations are not necessarily less abundant than core populations (Sagarin et al. 2006), although, as long as dispersal between populations is ensured, immigration from core habitats can sustain populations in habitats where the population growth rate is negative and so recruitment could never compensate for mortality (Kawecki 2008). Albeit some local extinction observed in Western Alps (Buffet and Dumont-Dayot 2011), Rock ptarmigan still lives in a metapopulation structure (Caizergues et al. 2003a), where sub-populations are located within dispersal distance capabilities (Favaron et al. 2006), so that immigration from inner Alps helping CACN4 population performing equally well cannot be excluded. It is clear that the observed lack of plasticity exposes the population to a high risk of extinction if climatic conditions would be increasingly unfavourable. A summer temperature increase of 1° C (Rebetez and Reinhard 2008) or 1.6° C (Gobiet et al. 2014) by mid-XXI century would result in a upward shift of, respectively, 192-308m, assuming an elevational temperature gradient of -0.52° C/100 m (Maggini et al. 2011), which would not be possible in CACN4 due to the local low upper limit of the range.

Being a cold-adapted species, Rock ptarmigan biogeographic history is markedly influenced by glacial pulses of the Pleistocene (Holder et al. 1999, 2000; Kozma et al. 2016). Reconstruction of past population fluctuations in Northern Europe by genome sequencing highlighted that Rock ptarmigan experienced a severe population bottleneck during the last glacial maximum (20000 years BP), caused by extensive ice cover which limited suitable habitat (Kozma et al. 2016). During the same period, Central and Southern Europe offered vast suitable territories of cold semi-desert, which started disappearing over the last 10000–15000 (Caizergues et al. 2003a). Hence, geographic and ecological marginality of CACN4 occurred in very recent times on the evolutionary scale and likely the period comprised between the onset of marginality and the current situation is too short for genotypic adaptation and possibly also for phenotypic plasticity to appear (Ghalambor et al. 2007).

CONCLUSIONS

4.5 The need for robust monitoring

This PhD project led to an increase of knowledge of the conservation status of Italian Alpine Galliforms, with an in-depth analysis on marginal populations. According to the two studies focused on the estimation of medium term national trends (Chapter 1 and 2), I was able to confirm the validity of current IUCN status classification of the three target species (LC for the Black grouse, VU for Rock ptarmigan and Rock partridge). However, the available dataset proved to be still inadequate for robust studies on population dynamics and the evaluation of the effects of environmental factors related to global change. Currently, Italy should quickly fill the gap with other Alpine nations, which own long term standardized data series and have a national coordination on Galliform management (e.g. Observatoire des Galliformes de Montagne in France, Swiss Ornithological Institute in Switzerland). Both bag and count data of Italian populations of Alpine Galliforms are subject to species-specific flaws and are possibly influenced by different game management policies enforced. Given that Alpine Galliforms all listed in the Annex I and II of the Birds Directive, I highlight the need for a national survey scheme and national game management guidelines applied uniformly across the Italian Alps, in order to allow the elaboration of national management and conservation strategies on solid bases. The integration of count and bag data and the use of state-space models represented an *ad hoc* solution to limit uncertainty on the estimation of population trends and to account for estimation errors, but it is a solution to obtain the best out of poor data. However, since 2015, there is an ongoing process of transferring of the hunting authority from provinces previously in charge to regions, which have already started drafting guidelines. This could be considered a first step towards a national standardisation.

Here below I summarised some potential improvements to current enforced game management.

Data gathering.

Count and bag data should be archived in a national georeferenced database, on the model of ungulate management, for which Italy has already defined a protocol on data flow from local administrations to national institutions. This would improve the evaluation of the conservation status and the hunting pressure at national scale, quickly providing information to researchers and policymakers, in compliance with reporting requirements of the European Union. Notable examples of national hunting statistics and wildlife data databases exist in Fennoscandian (eg. Finland, Helle et al. 2016; Norway, www.ssb.no) as well as Alpine countries (France, www.observatoire-galliformes-montagne.com; Switzerland, www.vogelwarte.ch).

Counts.

Sampling areas should be standardised across administrations in terms of number and average size. The extent of each area should be large enough include both winter/spring and summer/autumn ranges, according to the species eco-ethology. In a perspective of resource optimisation, we suggest the choice of few large areas instead of several small. Within each sampling area, spring and summer counts parcels should be defined. Spring counts should become mandatory and annual shooting plans should be set taking into account not only the breeding success but also population trends deriving from spring counts. Sampling methods (point counts, line transects) should be standardised whenever possible; the choice should take into account local environmental conditions and human resources available. We recommend the application of repeated counts, at least in spring, in order to minimize bias from weather conditions and to allow the utilisation of population modelling techniques that include species' detectability (e.g. N-mixture models, Kéry and Schaub 2012). Collected data variables should be standardised, with specification of sex and age when possible. Derived parameters such as breeding success or population density should be calculated from defined criteria.

Hunting statistics and plans.

Shooting plans should be set with standardised criteria, taking into account, as already mentioned, population trends, population densities and breeding success. Similarly to counts, we recommend the collection of sex and age information of harvested birds in order to estimate sex ratio and to compare juvenile recruitment from summer counts and game bags. Finally, information of number of hunting licenses and hunting days in each hunting district should be collected at national scale to allow hunting effort estimation as hunting person-days.

The application of these "good practices" would lead to a robust monitoring of conservation statuses both at national and local scale in compliance with the Birds' Directive demands.

4.6 Global change threatening trailing edge populations

In Chapter 3 and 4 we focused on the trailing edge of Black grouse and Rock ptarmigan distribution on the Alps. The identification of marginal populations living at lower elevations as 'trailing edge' finds its basis on the fact there is evidence of distribution shifts along that elevational gradient caused by the two major sources of habitat change, climate and land use, both acting from below. Hence, for populations strongly constrained in latitudinal dispersal such as Alpine Galliforms, we observe a 'leading edge' at higher elevations, inhabited by sub-populations which settle in new areas, and a 'trailing edge', where population experience the harshest change and abandon former habitats (Thomas et al. 2001; Hampe and Petit 2005). This is quite a straightforward concept when dealing with climate change, confirmed by an overwhelming number of studies which analysed and predicted the effects of warmer temperatures at various scale of the biological diversity, from intraspecific genetic heterogeneity to biomes (Walther et al. 2005; Pearman et al. 2011; Gottfried et al. 2012; Pauls et al. 2013; Vittoz et al. 2013; Thuiller et al. 2014). In this case, I evidenced that similar dynamics are determined by land cover changes presumably triggered by land abandonment, which resulted more effective in the pre-Alpine areas. The extent of the observed reduction in habitat suitability was impressively high, but the elevational gradient in mountain areas speed up the migration of habitats. Indeed, since habitats are juxtaposed in elevational belts often enclosed in less than 1 km, plant migrating capabilities through seed dispersal exceed the displacement required to colonize new habitats (Jump et al. 2009). Land use change is potentially even more detrimental than climate change to Black grouse. Even if differential warming is recorded among elevational belts (Acquaotta et al. 2015), the net distribution range should not change substantially as long as trailing edge retractions are compensated by an advancing leading edge. In the case of Lombardy, habitat suitability was halved in 35 years, since the leading edge upwards expansion was almost negligible if compared to the extensive loss detected at the trailing edge. As a consequence, the sharpest decline recorded among 9 biogeographic regions in Chapter 2 was seen in the Lombardy pre-Alps indeed (-66% habitat suitability), equal to an estimated 57% abundance loss between 1996 and 2014 (which raise to 75% based on lower CI). Conversely, in NE inner Alps, where habitat reduction was extremely limited, the species showed a stable trend.

Trailing edge have a great importance for biodiversity and the conservation of marginal populations deserve high priority (Hampe and Petit 2005). Appropriate conservation strategies need to be designed that consider the peculiarities of trailing edge populations. For instance, conservation strategies should be directed towards the detection and maintenance of the greatest possible number of local populations, regardless of their size or performance, instead of focusing on the most viable core populations. Therefore, I recommend that for Black grouse these strategies should take into account habitat management measures targeted at increasing structural diversity in the outer Alpine belt especially in larch sparse woods (Patthey et al. 2012), promoting whenever possible traditional farming which helps suitable habitats self-maintaining with limited expense (Losinger et al. 2011). In France this strategy has long tradition and more than 120 interventions were reported from 1989 to 2003 (Novoa et al. 2002). Successful outcomes of such habitat management operations in terms of increased breeding success were reported (Novoa et al. 2002; Rotelli 2014). Management resources should be allocated in geographic regions where shrub encroachment represents a major biodiversity conservation issue (Braunisch et al. 2016).

In case of Rock ptarmigan, short and medium term conservation of its trailing edge cannot rely on habitat management as for Black grouse, since the major constraint acting directly and indirectly on its distribution is temperature (Revermann et al. 2012). However, by evidencing a lack of phenotypic plasticity of marginal populations, I would recommend to take into account also for a core-marginal gradient when planning conservation strategies. Areas located on the distribution edge should be prioritized, although their demographic parameters may reveal a healthy population. For example, hunting in marginal areas could be strongly limited or even banned to avoid a further source of stress to populations, as well activities causing high disturbance such as hiking or off-ski pist could be regulated (Formenti et al. 2015; Chamberlain et al. 2016). Ferrarini et al. (2017) recently evidenced that the predicted climate-driven upward shift of treelines by the end of XXI century will be 10-fold more considerable at lower elevations (<1900 m) than high elevations (>2400 m). Thus, as for Black grouse, direct subventions for maintaining pastures above treelines could be allocated selectively in marginal areas where Rock ptarmigan lives on average at lower elevations (es. NE Italy, Brichetti and Fracasso 2004).

LITERATURE CITED

Aanes S, Engen S, SÆther B-E, et al (2002) Sustainable harvesting strategies of willow ptarmigan in a fluctuating environment. Ecol Appl 12:281–290

Abadi F, Gimenez O, Arlettaz R, Schaub M (2010a) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. Ecology 91:7–14. doi: 10.1890/08-2235.1

Abadi F, Gimenez O, Ullrich B, et al (2010b) Estimation of immigration rate using integrated population models. J Appl Ecol 47:393–400. doi: 10.1111/j.1365-2664.2010.01789.x

Abegg B, Agrawala S, Crick F, De Montfalcon A (2007) Climate change impacts and adaptation in winter tourism. In: Agrawala S (ed) Climate Change in the European Alps. OECD Publishing, p 131

Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical background in species distribution modelling. J Biogeogr 39:1383–1390. doi: 10.1111/j.1365-2699.2012.02713.x

Acquaotta F, Fratianni S, Garzena D (2015) Temperature changes in the North-Western Italian Alps from 1961 to 2010. Theor Appl Climatol 122:619–634. doi: 10.1007/s00704-014-1316-7

Aebischer NJ (1991) Sustainable yields: gamebirds as a harvestable resource. Gibier Faune Sauvage 8:335–351

Aebischer NJ, Baines D (2008) Monitoring gamebird abundance and productivity in the UK: The GWCT long-term datasets. Rev Catalana D'Ornitologia 24:30

Agnelli P, Martinoli A, Patriarca E, et al (2006) Guidelines for bat monitoring: methods for the study and conservation of bats in Italy. Min. Ambiente - Ist. Naz. Fauna Selvatica, Rome and Ozzano dell'Emilia (Bologna), Italy

Agostinelli C, Lund U (2017) R package "circular": Circular Statistics

Agrawala S, Organisation for Economic Co-operation and Development (eds) (2007) Climate change in the European Alps: adapting winter tourism and natural hazards management. Organisation for Economic Co-operation and Development, Paris

Anderson AS, Marques TA, Shoo LP, Williams SE (2015) Detectability in audio-visual surveys of tropical rainforest birds: the influence of species, weather and habitat characteristics. PloS One 10:e0128464

Anderson DR, Burnham KP (1981) Bobwhite Population Responses to Exploitation: Two Problems. J Wildl Manag 45:1052–1054. doi: 10.2307/3808129

Anderson-Sprecher R, Ledolter J (1991) State-Space Analysis of Wildlife Telemetry Data. J Am Stat Assoc 86:596–602. doi: 10.1080/01621459.1991.10475084

Andreev AV (1999) Energetics and survival of birds in extreme environments. Ostrich 70:13–22. doi: 10.1080/00306525.1999.9639745

Andrén H (1994) Effects of Habitat Fragmentation on Birds and Mammals in Landscapes with Different Proportions of Suitable Habitat: A Review. Oikos 71:355–366. doi: 10.2307/3545823

Andrén H, Angelstam P, Lindström E, Widén P (1985) Differences in Predation Pressure in Relation to Habitat Fragmentation: An Experiment. Oikos 45:273. doi: 10.2307/3565714

Anthelme F, Grossi J-L, Brun J-J, Didier L (2001) Consequences of green alder expansion on vegetation changes and arthropod communities removal in the northern French Alps. For Ecol Manag 145:57–65. doi: 10.1016/S0378-1127(00)00574-0

Apollonio M, Andersen R, Putman R (eds) (2010) European Ungulates and their Management in the 21st Century. Cambridge University Press, Cambridge

Archaux F (2004) Breeding upwards when climate is becoming warmer: no bird response in the French Alps. Ibis 146:138–144. doi: 10.1111/j.1474-919X.2004.00246.x

Arlettaz R, Patthey P, Baltic M, et al (2007) Spreading free-riding snow sports represent a novel serious threat for wildlife. Proc R Soc B Biol Sci 274:1219–1224. doi: 10.1098/rspb.2006.0434

Arlettaz R, Patthey P, Braunisch V (2013) Impacts of Outdoor Winter Recreation on Alpine Wildlife and Mitigation Approaches: A Case Study of the Black Grouse. Impacts Ski Relat Winter Recreat Act Mt Environ Eds C Rixen Rolando S 137–154

ARPA Lombardia (2003) Annale idrologico. http://ita.arpalombardia.it/ITA/settori/idrografia/annale_idro1.asp. Accessed 6 Feb 2017

Arrigoni degli Oddi E (1899) Note ornitologiche sulla provincia di Verona. Atti Della Soc It Sc Nat 38:75–191

Baines D, Hudson PJ (1995) The decline of Black Grouse in Scotland and northern England. Bird Study 42:122–131. doi: 10.1080/00063659509477158

Baltic M, Jenni-Eiermann S, Arlettaz R, Palme R (2005) A Noninvasive Technique to Evaluate Human-Generated Stress in the Black Grouse. Ann N Y Acad Sci 1046:81–95. doi: 10.1196/annals.1343.008

Baratti M, Migliorini M, Bernini F (2000) Effetti dell'innevamento artificiale sugli Acari oribatei (Acari, Oribatida) delle piste sciabili del Monte Bondone (Trentino, Italia). Studi Trentini Sci Nat Biol 75:147–159

Barbet-Massin M, Thuiller W, Jiguet F (2012) The fate of European breeding birds under climate, land-use and dispersal scenarios. Glob Change Biol 18:881–890. doi: 10.1111/j.1365-2486.2011.02552.x

Barilani M, Bernard-Laurent A, Mucci N, et al (2007) Hybridisation with introduced chukars (Alectoris chukar) threatens the gene pool integrity of native rock (A. graeca) and red-legged (A. rufa) partridge populations. Biol Conserv 137:57–69. doi: 10.1016/j.biocon.2007.01.014

Barnagaud J-Y, Crochet PA, Magnani Y, et al (2010) Short-term response to the North Atlantic Oscillation but no long-term effects of climate change on the reproductive success of an alpine bird. J Ornithol 152:631–641. doi: 10.1007/s10336-010-0623-8

Barnes RFW (1987) Long-Term Declines of Red Grouse in Scotland. J Appl Ecol 24:735–741. doi: 10.2307/2403977

Bebi P, Seidl R, Motta R, et al (2017) Changes of forest cover and disturbance regimes in the mountain forests of the Alps. For Ecol Manag 388:43–56. doi: 10.1016/j.foreco.2016.10.028

Bellard C, Bertelsmeier C, Leadley P, et al (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377. doi: 10.1111/j.1461-0248.2011.01736.x

Beniston M (2012) Is snow in the Alps receding or disappearing?: Is snow in the Alps receding or disappearing? Wiley Interdiscip Rev Clim Change 3:349–358. doi: 10.1002/wcc.179

Beniston M, Stephenson DB, Christensen OB, et al (2007) Future extreme events in European climate: an exploration of regional climate model projections. Clim Change 81:71–95. doi: 10.1007/s10584-006-9226-z

Bernard-Laurent A (1991) Migrant Rock Partridges (Alectoris graeca saxatilis) in the southern French Alps. J Für Ornithol 132:220–223. doi: 10.1007/BF01647281

Bernard-Laurent A (1994a) Méthode de dénombrement des perdrix bartavelle mâles au chant et présentation des résultats

Bernard-Laurent A (1994b) Statut, évolution et facteurs limitant les populations de tétras-lyre (Tetrao tetrix) en France: synthèse bibliographique. Gibier Faune Sauvage 11:205–239

Bernard-Laurent A, Auliac P, Douvre P, et al (2001) Risques de pollution génétique des populations de perdrix bartavelle: Bilan d'une enquête sur les lâchers de perdrix rouge dans les Alpes francaises. Faune Sauvage 254:10–15

Bernard-Laurent A, Corti R, Ellison LN, et al (1998) Le Tétras-lyre. ONCFS Publications

Bernard-Laurent A, De Franceschi PF (1994) Statut, évolution et facteurs limitant les populations de perdrix bartavelle (Alectoris graeca): synthèse bibliographique. Gibier Faune Sauvage 11:267–307

Bernard-Laurent A, Laurent J-L (1984) Méthode de recensement des perdrix bartavelles (Alectoris graeca saxatilis Bechstein 1805) au printemps; applications dans les Alpes-Maritimes. Gibier Faune Sauvage 4:69–85

Bernard-Laurent A, Léonard Y (2000) Vulnerability of an alpine population of rock partridge (Alectoris graeca saxatilis) to climatic events: evaluation with deterministic and stochastic models. Game Wildl Sci 17:63–69

Besbeas P, Freeman SN, Morgan BJT, Catchpole EA (2002) Integrating Mark–Recapture–Recovery and Census Data to Estimate Animal Abundance and Demographic Parameters. Biometrics 58:540–547. doi: 10.1111/j.0006-341X.2002.00540.x

Besbeas P, Lebreton J-D, Morgan BJT (2003) The efficient integration of abundance and demographic data. J R Stat Soc Ser C Appl Stat 52:95–102. doi: 10.1111/1467-9876.00391

Bibby C, Burgess N, Hill D, Mustoe S (2000) Bird Census Techniques - 2nd Edition. Academic Press

BirdLife International (2016) The IUCN Red List of Threatened Species 2016: e.T22679464A113623562.

BirdLife International (2015a) European Red List of Birds. Office for Official Publications of the European Communities, Luxembourg

BirdLife International (2004) Birds in the European Union - a status assessment. BirdLife International, Wageningen, The Netherlands

BirdLife International (2015b) Lyrurus tetrix (Black Grouse). Supplementary material. In: European Red List of Birds. Office for Official Publications of the European Communities, Luxembourg

BirdLife International (2015c) Lagopus muta (Rock Ptarmigan). Supplementary material. In: European Red List of Birds. Office for Official Publications of the European Communities, Luxembourg

BirdLife International (2015d) Alectoris graeca (Rock Partridge). Supplementary material. In: European Red List of Birds. Office for Official Publications of the European Communities, Luxembourg

Bisi F, D’Acunto D, De Franceschi C, et al (2012) Catture di pernice bianca in aree protette e venabili. Progetto n 88. Galliformi alpini. I galliformi alpini sulle alpi occidentali come indicatori ambientali: Monitoraggio, conservazione e gestione delle specie. Programma Alcotra 2007-2013 (Rock ptarmigan captures in protected areas and hunting grounds. Project n 88. Alpine Galliforms. Alpine Galliforms in the Western Alps as environmental indicators: monitoring, conservation and species management. Alcotra Program 2007–2013) (in Italian). Regione Piemonte, Turin, ONCFS, Paris, CNR, Rome and Regione Autonoma Valle d’Aosta, Aosta

Bocca M, Caprio E, Chamberlain D, Rolando A (2013) The winter roosting and diet of Black Grouse Tetrao tetrix in the north-western Italian Alps. J Ornithol 155:183–194. doi: 10.1007/s10336-013-1000-1

Boggs C, Norris E, Steen JB (1977) Behavioural and physiological temperature regulation in young chicks of the willow grouse (Lagopus lagopus). Comp Biochem Physiol A Physiol 58:371–372. doi: 10.1016/0300-9629(77)90157-8

Bolli JC, Rigling A, Bugmann H, others (2007) The influence of changes in climate and land-use on regeneration dynamics of Norway spruce at the treeline in the Swiss Alps. Silva Fenn 41:55

Bolliger J, Kienast F, Soliva R, Rutherford G (2007) Spatial sensitivity of species habitat patterns to scenarios of land use change (Switzerland). Landsc Ecol 22:773–789. doi: 10.1007/s10980-007-9077-7

Bossert A (1977) Bestandesaufnahme am Alpenschneehuhn Lagopus mutus im Aletschgebiet. Ornithol Beob 74:95–98

Both C, Visser ME (2011) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298

Boulangeat I, Georges D, Dentant C, et al (2014) Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. Ecography 37:1230–1239. doi: 10.1111/ecog.00694

Brambilla M, Pedrini P, Rolando A, Chamberlain DE (2016) Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. J Biogeogr 43:2299–2309. doi: 10.1111/jbi.12796

Braun-Blanquet J (1958) Über die obersten Grenzen pflanzlichen Lebens im Gipfelbereich des Schweizerischen Nationalparks. Komm Schweiz Naturforsch Ges Wiss Erforsch Natl 6:119–142

Braunisch V, Patthey P, Arlettaz R (2016) Where to Combat Shrub Encroachment in Alpine Timberline Ecosystems: Combining Remotely-Sensed Vegetation Information with Species Habitat Modelling. PLOS ONE 11:e0164318. doi: 10.1371/journal.pone.0164318

Braunisch V, Patthey P, Arlettaz R (2011) Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. Ecol Appl 21:955–967

Brichetti P (1990) Coturnice (Alectoris graeca). In: Atlante degli uccelli nidificanti in Lombardia 1983-1987. Editoriale Ramperto

Brichetti P, Fracasso G (2004) Ornitologia italiana. 2. Tetraonidi - Scolopacidi. Oasi Alberto Perdisa

Brommer JE (2004) The range margins of northern birds shifting polewards. Ann Zool Fenn 41:391–397

Brooks SP, Gelman A (1998) General Methods for Monitoring Convergence of Iterative Simulations. J Comput Graph Stat 7:434–455. doi: 10.1080/10618600.1998.10474787

Brown JH, Mehlman DW, Stevens GC (1995) Spatial Variation in Abundance. Ecology 76:2028–2043. doi: 10.2307/1941678

Buffet N, Dumont-Dayot E (2011) Évolution de la répartition communale du petit gibier de montagne en France - Décennie 2000-2009. Faune Sauvage 290

Burel F, Baudry J (1995) Species biodiversity in changing agricultural landscapes: A case study in the Pays d'Auge, France. Agric Ecosyst Environ 55:193–200. doi: 10.1016/0167-8809(95)00614-X

Büttner G, Soukup T, Kosztra B (2014) CLC2012 addendum to CLC2006 technical guidelines. European Environmental Agency, Copenhagen, DK

Caizergues A, Bernard-Laurent A, Brenot J-F, et al (2003a) Population genetic structure of rock ptarmigan Lagopus mutus in Northern and Western Europe. Mol Ecol 12:2267–2274. doi: 10.1046/j.1365-294X.2003.01889.x

Caizergues A, Ellison LN (2002) Natal dispersal and its consequences in Black Grouse Tetrao tetrix. Ibis 144:478–487. doi: 10.1046/j.1474-919X.2002.00040.x

Caizergues A, Ellison LN (1997) Survival of Black grouse Tetrao Tetrix in the French Alps. Wildl Biol 3:177–186

Caizergues A, Rätti O, Helle P, et al (2003b) Population genetic structure of male black grouse (Tetrao tetrix L.) in fragmented vs. continuous landscapes. Mol Ecol 12:2297–2305. doi: 10.1046/j.1365-294X.2003.01903.x

Camacho O, Dobremez L, Capillon A (2008) Shrub encroachment in pastures in the Alps. J Alp Res Rev Géographie Alp 89–100. doi: 10.4000/rga.575

Campbell JB, Wynne RH (2011) Introduction to remote sensing. Guilford Press

Cannone N, Pignatti S (2014) Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? Clim Change 123:201–214. doi: 10.1007/s10584-014-1065-8

Carroll SP (2008) Facing change: forms and foundations of contemporary adaptation to biotic invasions. Mol Ecol 17:361–372. doi: 10.1111/j.1365-294X.2007.03484.x

Cattadori IM, Haydon DT, Thirgood SJ, Hudson PJ (2003a) Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. Oikos 100:439–446. doi: 10.1034/j.1600-0706.2003.12072.x

Cattadori IM, Hudson PJ, Merler S, Rizzoli A (1999) Synchrony scale and temporal dynamics of rock partridge Alectoris graeca saxatilis populations in the Dolomites. J Anim Ecol 68:540–549

Cattadori IM, Ranci-Ortigosa G, Gatto M, Hudson PJ (2003b) Is the rock partridge Alectoris graeca saxatilis threatened in the Dolomitic Alps? Anim Conserv 6:71–81. doi: 10.1017/S136794300300310X

Cernusca A, Tappeiner U, Bayfield N (1999) Land-use Changes in European Mountain Ecosystems: ECOMONT - Concepts and Results, Europäische Akademie Bozen, Fachbereich Alpine Umwelt. Blackwell-Wiss.-Verl, Berlin

Chaloupka M, Balazs G (2007) Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. Ecol Model 205:93–109. doi: 10.1016/j.ecolmodel.2007.02.010

Chamberlain DE, Negro M, Caprio E, Rolando A (2013) Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. Biol Conserv 167:127–135. doi: 10.1016/j.biocon.2013.07.036

Chamberlain DE, Pedrini P, Brambilla M, et al (2016) Identifying key conservation threats to Alpine birds through expert knowledge. PeerJ 4:e1723. doi: 10.7717/peerj.1723

Chanin PRF, Jefferies DJ (1978) The decline of the otter Lutra lutra L. in Britain: an analysis of hunting records and discussion of causes. Biol J Linn Soc 10:305–328

Charmantier A, McCleery RH, Cole LR, et al (2008) Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population. Science 320:800–803. doi: 10.1126/science.1157174

Chauchard S, Beilhe F, Denis N, Carcaillet C (2010) An increase in the upper tree-limit of silver fir (Abies alba Mill.) in the Alps since the mid-20th century: A land-use change phenomenon. For Ecol Manag 259:1406–1415. doi: 10.1016/j.foreco.2010.01.009

Chee YE, Wintle BA (2010) Linking modelling, monitoring and management: an integrated approach to controlling overabundant wildlife. J Appl Ecol 47:1169–1178. doi: 10.1111/j.1365-2664.2010.01877.x

Chemini C, Giannelle D (1999) Pascolo e conservazione della biodiversità. In: Presente e futuro dei pascoli alpini in Europa. Franco Angeli, Milano, pp 36–48

Chemini C, Rizzoli A (2003) Land use change and biodiversity conservation in the Alps. J Mt Ecol 7:1–7

Chen I, Hill JK, Ohlemueller R, et al (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333:1019–1024. doi: 10.1126/science.1202702

Christensen TK (2005) Factors affecting the bag size of the common eider Somateria mollissima in Denmark, 1980–2000. Wildl Biol 11:89–99. doi: 10.2981/0909-6396(2005)11[89:FATBSO]2.0.CO;2

Clark JS, Bjørnstad ON (2004) Population Time Series: Process Variability, Observation Errors, Missing Values, Lags, and Hidden States. Ecology 85:3140–3150. doi: 10.1890/03-0520

Collini M (2011) La pernice bianca alpina (Lagopus muta helvetica): una sottospecie endemica in declino. Filogeografia, variabilità genetica e aspetti biologici.

Corti Mi (2004) L' alpeggio nelle Alpi lombarde tra passato e presente. In: SM Annali di San Michele. pp 31–155

Coulson T, Catchpole EA, Albon SD, et al (2001) Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. Science 292:1528–1531

CREN Rhône-Alpes (2009) Entre forêts et pelouses - Habitat de reproduction du tétras-lyre. CREN Rhône-Alpes

Crochet P-A (2000) Genetic structure of avian populations—allozymes revisited. Mol Ecol 9:1463–1469

Cromsigt JPGM, Rensburg SJ van, Etienne RS, Olff H (2009) Monitoring large herbivore diversity at different scales: comparing direct and indirect methods. Biodivers Conserv 18:1219–1231. doi: 10.1007/s10531-008-9506-1

D'Amen M, Bombi P (2009) Global warming and biodiversity: Evidence of climate-linked amphibian declines in Italy. Biol Conserv 142:3060–3067. doi: 10.1016/j.biocon.2009.08.004

Daughtry CST, Doraiswamy PC, Hunt ER, et al (2006) Remote sensing of crop residue cover and soil tillage intensity. Soil Tillage Res 91:101–108. doi: 10.1016/j.still.2005.11.013

Davis AJ, Hooten MB, Phillips ML, Doherty PF (2014) An integrated modeling approach to estimating Gunnison sage-grouse population dynamics: combining index and demographic data. Ecol Evol 4:4247–4257. doi: 10.1002/ece3.1290

Davis MB, Shaw RG (2001) Range Shifts and Adaptive Responses to Quaternary Climate Change. Science 292:673–679. doi: 10.1126/science.292.5517.673

De Franceschi PF (1994) Status, geographical distribution and limiting factors of black grouse (Tetrao tetrix) in Italy. Gibier Faune Sauvage 11:185–205

de Valpine P, Hastings A (2002) Fitting population models incorporating process noise and observation error. Ecol Monogr 72:57–76

Decout S, Signer J (2010) Habitat Distribution and Connectivity for Black Grouse (Tetrao tetrix) in the Alps del Hoyo J, Elliott A, Sargatal J, et al (2017) Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona

Della Marianna G, Gusmeroli F, Puccio C (2004) Gli Alpeggidella Comunità Montana Valtellina di Sondrio. Ufficio Agricoltura e Foreste Comunità Montana Valtellina di Sondrio

Desmet J-F (2014) Quel avenir pour le Lagopèede alpin en France? In: Gauthier-Clerc M, Mesléard F, Blondel J (eds) Sciences de la conservation. De Boeck, Paris, pp 210–211

Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not fast enough. Proc R Soc Lond B Biol Sci 275:2743–2748. doi: 10.1098/rspb.2008.0878

DeWitt TJ, Scheiner SM (2004) Phenotypic plasticity: functional and conceptual approaches. Oxford University Press

Dirnböck T, Dullinger S, Grabherr G (2003) A regional impact assessment of climate and land-use change on alpine vegetation. J Biogeogr 30:401–417. doi: 10.1046/j.1365-2699.2003.00839.x

DLG (2005) Land abandonment, biodiversity and the CAP. Government Service for Land and Water Management of the Netherlands

Dobson A (2005) Monitoring global rates of biodiversity change: challenges that arise in meeting the Convention on Biological Diversity (CBD) 2010 goals. Philos Trans R Soc Lond B Biol Sci 360:229–241. doi: 10.1098/rstb.2004.1603

Drovetski SV (2003) Plio-Pleistocene climatic oscilations, Holarctic biogeography and speciation in an avian subfamily. J Biogeogr 30:1173–1181

Dullinger S, Dirnböck T, Grabherr G (2003) Patterns of Shrub Invasion into High Mountain Grasslands of the Northern Calcareous Alps, Austria. Arct Antarct Alp Res 35:434–441. doi: 10.1657/1523-0430(2003)035[0434:POSIIH]2.0.CO;2

Durand Y, Giraud G, Laternser M, et al (2009) Reanalysis of 47 Years of Climate in the French Alps (1958–2005): Climatology and Trends for Snow Cover. J Appl Meteorol Climatol 48:2487–2512. doi: 10.1175/2009JAMC1810.1

Elith J, Phillips SJ, Hastie T, et al (2011) A statistical explanation of MaxEnt for ecologists: Statistical explanation of MaxEnt. Divers Distrib 17:43–57. doi: 10.1111/j.1472-4642.2010.00725.x

Ellison L, Léonard P, Menoni E (1988) Evolution des effectifs de tétras lyre sur un territoire de chasse. Gibier Faune Sauvage 5:309–320

Ellison L, Magnani Y (1985) Eléments de dynamique de population du Tétras lyre (Tetrao tetrix) dans les Alpes françaises. Gibier Faune Sauvage 4:63–84

Ellison LN (1991) Shooting and Compensatory Mortality in Tetraonids. Ornis Scand 22:229. doi: 10.2307/3676595

Ellison LN, Ménoni E, Léonard P (1989) Déplacements d'adultes de tétras lyre (Tetrao tetrix) en automne et en hiver. Gibier Faune Sauvage 6:245–260

Elmhagen B, Hellström P, Angerbjörn A, Kindberg J (2011) Changes in Vole and Lemming Fluctuations in Northern Sweden 1960–2008 Revealed by Fox Dynamics. Ann Zool Fenn 48:167–179. doi: 10.5735/086.048.0305

Elmhagen B, Kindberg J, Hellström P, Angerbjörn A (2015) A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. AMBIO 44:39–50. doi: 10.1007/s13280-014-0606-8

Elsasser H, Messerli P (2001) The Vulnerability of the Snow Industry in the Swiss Alps. Mt Res Dev 21:335–339. doi: 10.1659/0276-4741(2001)021[0335:TVOTSI]2.0.CO;2

Elton C, Nicholson M (1942) The Ten-Year Cycle in Numbers of the Lynx in Canada. J Anim Ecol 11:215. doi: 10.2307/1358

Erikstad KE, Andersen R (1983) The Effect of Weather on Survival, Growth Rate and Feeding Time in Different Sized Willow Grouse Broods. Ornis Scand 14:249–252. doi: 10.2307/3676311

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Evol Syst 34:487–515. doi: 10.1146/annurev.ecolsys.34.011802.132419

Falcucci A, Maiorano L, Boitani L (2006) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. Landsc Ecol 22:617–631. doi: 10.1007/s10980-006-9056-4

Farina A (1991) Recent changes of the mosaic patterns in a montane landscape (north Italy) and consequences on vertebrate fauna. Options Méditerranéennes—Série Sémin 15:121–134

Fasel M, Zbinden N (1983) Kausalanalyse zum Verlauf der Suedlichen Arealgrenze des Alpenschneehuhns Lagopus mutus im Tessin. Ornithol Beob 80:231–246

Favaron M, Scherini GC, Preatoni D, et al (2006) Spacing behaviour and habitat use of rock ptarmigan (Lagopus mutus) at low density in the Italian Alps. J Ornithol 147:618–628. doi: 10.1007/s10336-006-0087-z

Ferrarini A, Alatalo JM, Gustin M (2017) Climate change will seriously impact bird species dwelling above the treeline: A prospective study for the Italian Alps. Sci Total Environ. doi: 10.1016/j.scitotenv.2017.03.027

Ferreira C, Paupério J, Alves PC (2010) The usefulness of field data and hunting statistics in the assessment of wild rabbit (Oryctolagus cuniculus) conservation status in Portugal. Wildl Res 37:223–229. doi: 10.1071/WR09137

Fischer M, Rudmann-Maurer K, Weyand A, Stöcklin J (2008) Agricultural Land Use and Biodiversity in the Alps. Mt Res Dev 28:148–155. doi: 10.1659/mrd.0964

Forbey JS, Wiggins NL, Frye GG, Connelly JW (2013) Hungry grouse in a warming world: emerging risks from plant chemical defenses and climate change. Wildl Biol 19:374–381. doi: 10.2981/13-014

Forcey GM, Anderson JT, Ammer FK, Whitmore RC (2006) Comparison of Two Double-Observer Point-Count Approaches for Estimating Breeding Bird Abundance. J Wildl Manag 70:1674–1681. doi: 10.2193/0022-541X(2006)70[1674:COTDPA]2.0.CO;2

Formenti N, Viganó R, Bionda R, et al (2015) Increased hormonal stress reactions induced in an Alpine Black Grouse (Tetrao tetrix) population by winter sports. J Ornithol 156:317–321. doi: 10.1007/s10336-014-1103-3

Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. PLOS ONE 9:e97122. doi: 10.1371/journal.pone.0097122

Franzetti B, Toso S (2009) Sintesi dello stato di conservazione delle specie oggetto di prelievo venatorio ai sensi della legge 11 febbraio 1992 n. 157 e successive modificazioni. ISPRA

Freeman SN, Crick HQP (2003) The decline of the Spotted Flycatcher Muscicapa striata in the UK: an integrated population model. Ibis 145:400–412. doi: 10.1046/j.1474-919X.2003.00177.x

Furrer R, Schaub M, Bossert A, et al (2016) Variable decline of Alpine Rock Ptarmigan (Lagopus muta helvetica) in Switzerland between regions and sites. J Ornithol 1–10. doi: 10.1007/s10336-016-1324-8

Garbarino M, Lingua E, Subirà MM, Motta R (2011) The larch wood pasture: structure and dynamics of a cultural landscape. Eur J For Res 130:491–502. doi: 10.1007/s10342-010-0437-5

García-González R, Aldezabal A, Laskurain NA, et al (2016) Influence of Snowmelt Timing on the Diet Quality of Pyrenean Rock Ptarmigan (Lagopus muta pyrenaica): Implications for Reproductive Success. PLOS ONE 11:e0148632. doi: 10.1371/journal.pone.0148632

Gates CE, Marshall WH, Olson DP (1968) Line Transect Method of Estimating Grouse Population Densities. Biometrics 24:135. doi: 10.2307/2528465

Géhin B, Montadert M (2016) Bilans demographique 2016 des Galliformes de montagne - Massif Alpin. Observatore des Galliformes de Montagne

Gehrig R (2006) The influence of the hot and dry summer 2003 on the pollen season in Switzerland. Aerobiologia 22:27–34. doi: 10.1007/s10453-005-9013-8

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? J Veg Sci 18:571–582

Gehrt SD, Hubert Jr GF, Ellis JA (2002) Long-term population trends of raccoons in Illinois. Wildl Soc Bull 457–463

Gellrich M, Baur P, Koch B, Zimmermann NE (2007) Agricultural land abandonment and natural forest re-growth in the Swiss mountains: A spatially explicit economic analysis. Agric Ecosyst Environ 118:93–108. doi: 10.1016/j.agee.2006.05.001

Gelman A, Meng X-L, Stern H (1996) Posterior Predictive Assessment of Model Fitness Via Realized Discrepancies. Stat Sin 6:733–807

George L, Macpherson JL, Balmforth Z, Bright PW (2011) Using the dead to monitor the living: can road kill counts detect trends in mammal abundance? Appl Ecol Environ Res 9:27–41

Ghalambor CK, McKAY JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407. doi: 10.1111/j.1365-2435.2007.01283.x

Gienapp P, Teplitsky C, Alho JS, et al (2008) Climate change and evolution: disentangling environmental and genetic responses. Mol Ecol 17:167–178. doi: 10.1111/j.1365-294X.2007.03413.x

Giglioli HE (1891) Primo resoconto dei risultati dell'inchiesta ornitologica in Italia. Parte III, Le Monnier. Firenze

Gilks WR, Richardson S, Spiegelhalter DJ (eds) (1996) Monte Carlo Markov Chain in practice. Chapman & Hall, London

Gimenez O, Lebreton J-D, Gaillard J-M, et al (2012) Estimating demographic parameters using hidden process dynamic models. Theor Popul Biol 82:307–316. doi: 10.1016/j.tpb.2012.02.001

Gimenez O, Rossi V, Choquet R, et al (2007) State-space modelling of data on marked individuals. Ecol Model 206:431–438. doi: 10.1016/j.ecolmodel.2007.03.040

Gobiet A, Kotlarski S, Beniston M, et al (2014) 21st century climate change in the European Alps—A review. Sci Total Environ 493:1138–1151. doi: 10.1016/j.scitotenv.2013.07.050

Gomarasca MA (2004) Elementi di geomatica. AIT (Associazione Italiana di Telerilevamento)

González-Gallina A, Benítez-Badillo G, Hidalgo-Mihart MG, et al (2016) Roadkills as a complementary information source for biological surveys using rodents as a model. J Mammal 97:145–154. doi: 10.1093/jmammal/gyv165

Gottfried M, Pauli H, Futschik A, et al (2012) Continent-wide response of mountain vegetation to climate change. Nat Clim Change 2:111–115. doi: 10.1038/nclimate1329

Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature 369:448

Graf R, Bollmann K, Sachot S, et al (2006) On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. Ecography 29:319–328

Greenberg RS (1990) Ecological plasticity, neophobia, and resource use in birds. Stud Avian Biol 13:431–437

Greenwood JJD, Robinson RA (2006) Principles of sampling. In: Ecological Census Techniques: A Handbook. Cambridge University Press, p 446

Grime JP (2006) Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons

Guo Q, Taper M, Schoenberger M, Brandle J (2005) Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108:47–57. doi: 10.1111/j.0030-1299.2005.13149.x

Habel JC, Assmann T (2009) Relict species: phylogeography and conservation biology. Springer Science & Business Media

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecol Lett 8:461–467. doi: 10.1111/j.1461-0248.2005.00739.x

Hamr J (1988) Disturbance Behaviour of Chamois in an Alpine Tourist Area of Austria. Mt Res Dev 8:65. doi: 10.2307/3673407

Hancock M, Baines D, Gibbons D, et al (1999) Status of male Black Grouse Tetrao tetrix in Britain in 1995–96. Bird Study 46:1–15. doi: 10.1080/00063659909461110

Hannon SJ, Martin K (2006) Ecology of juvenile grouse during the transition to adulthood. J Zool 269:422–433. doi: 10.1111/j.1469-7998.2006.00159.x

Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol Lett 12:1040–1049. doi: 10.1111/j.1461-0248.2009.01355.x

Haslett JR (1997) Insect Communities and the Spatial Complexity of Mountain Habitats. Glob Ecol Biogeogr Lett 6:49. doi: 10.2307/2997526

Hayward MW (2011) Using the IUCN Red List to determine effective conservation strategies. Biodivers Conserv 20:2563–2573. doi: 10.1007/s10531-011-0091-3

Hefley TJ, Tyre AJ, Blankenship EE (2013) Statistical indicators and state–space population models predict extinction in a population of bobwhite quail. Theor Ecol 6:319–331. doi: 10.1007/s12080-013-0195-3

Helle P, Ikonen K, Kantola A (2016) Wildlife monitoring in Finland: online information for game administration, hunters, and the wider public. Can J For Res 1–6. doi: 10.1139/cjfr-2015-0454

Henle K, Potts SG, Kunin WE, et al (2014) Scaling in ecology and biodiversity conservation. Pensoft Publishers, Sofia

Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quaternary. Philos Trans R Soc Lond B Biol Sci 359:183–195. doi: 10.1098/rstb.2003.1388

Hijmans RJ (2016) raster: Geographic Data Analysis and Modeling

Hijmans RJ, Phillips SJ, Leathwick J, Elith J (2017) dismo: Species Distribution Modeling

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. Nature 470:479–485. doi: 10.1038/nature09670

Höglund J, Larsson JK, Jansman HAH, Segelbacher G (2007) Genetic variability in European black grouse (Tetrao tetrix). Conserv Genet 8:239–243. doi: 10.1007/s10592-006-9158-1

Höglund J, Stohr S (1997) A Non-Lekking Population of Black Grouse Tetrao tetrix. J Avian Biol 28:184. doi: 10.2307/3677312

Holder K, Montgomerie R, Friesen VL (1999) A Test of the Glacial Refugium Hypothesis Using Patterns of Mitochondrial and Nuclear Dna Sequence Variation in Rock Ptarmigan (lagopus Mutus). Evolution 53:1936–1950. doi: 10.1111/j.1558-5646.1999.tb04574.x

Holder K, Montgomerie R, Friesen VL (2000) Glacial vicariance and historical biogeography of rock ptarmigan (Lagopus mutus) in the Bering region. Mol Ecol 9:1265–1278. doi: 10.1046/j.1365-294x.2000.01005.x

Holtmeier F-K, Broll G (2005) Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales: Treeline and environmental change. Glob Ecol Biogeogr 14:395–410. doi: 10.1111/j.1466-822X.2005.00168.x

Honnay O, Piessens K, Van Landuyt W, et al (2003) Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. Landsc Urban Plan 63:241–250. doi: 10.1016/S0169-2046(02)00194-9

Hörnell-Willebrand M, Marcström V, Brittas R, Willebrand T (2006) Temporal and spatial correlation in chick production of willow grouse Lagopus lagopus in Sweden and Norway. Wildl Biol 12:347–355. doi: 10.2981/0909-6396(2006)12[347:TASCIC]2.0.CO;2

Houghton JT, Intergovernmental Panel on Climate Change (eds) (2001) Climate change 2001: the scientific basis: contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge ; New York

Hudson P j., Cattadori I m., Boag B, Dobson A p. (2006) Climate disruption and parasite–host dynamics: patterns and processes associated with warming and the frequency of extreme climatic events. J Helminthol 80:175–182. doi: 10.1079/JOH2006357

Hudson PJ (1992) Grouse in Space and Time. Game Conservancy Limited

Huntley B, Collingham YC, Green RE, et al (2006) Potential impacts of climatic change upon geographical distributions of birds. Ibis 148:8–28. doi: 10.1111/j.1474-919X.2006.00523.x

Huntley B, Green RE, Collingham YC, Willis SG (2007) A Climatic Atlas of European Breeding Birds. Lynx Edicions, Barcelona

Hyndman RJ, Khandakar J (2008) Automatic time series forecasting: the forecast package for R. J Stat Softw 26:1–22

Immitzer M, Nopp-Mayr U, Zohmann M (2013) Effects of habitat quality and hiking trails on the occurrence of Black Grouse (Tetrao tetrix L.) at the northern fringe of alpine distribution in Austria. J Ornithol 155:173–181. doi: 10.1007/s10336-013-0999-3

Imperio S, Bionda R, Viterbi R, Provenzale A (2013) Climate Change and Human Disturbance Can Lead to Local Extinction of Alpine Rock Ptarmigan: New Insight from the Western Italian Alps. PLoS ONE 8:e81598. doi: 10.1371/journal.pone.0081598

Imperio S, Ferrante M, Grignetti A, et al (2010) Investigating population dynamics in ungulates: Do hunting statistics make up a good index of population abundance? Wildl Biol 16:205–214. doi: 10.2981/08-051

ISTAT (2013) La Superficie dei Comuni, delle Province e delle Regioni Italiane

IUCN (2001) IUCN Red List Categories and Criteria - Version 3.1 Second edition. Gland, Switzerland and Cambridge, UK: IUCN

Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven

Jenouvrier S, Barbraud C, Weimerskirch H (2003) Effects of climate variability on the temporal population dynamics of southern fulmars. J Anim Ecol 72:576–587. doi: 10.1046/j.1365-2656.2003.00727.x

Jetz W, Wilcove DS, Dobson AP (2007) Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLoS Biol 5:e157. doi: 10.1371/journal.pbio.0050157

Johnson FA, Moore CT, Kendall WL, et al (1997) Uncertainty and the Management of Mallard Harvests. J Wildl Manag 61:202. doi: 10.2307/3802429

Johnson RA (1968) Temperature regulation in the white-tailed ptarmigan Lagopus leucurus

Jonas T, Geiger F, Jenny H (2008) Mortality pattern of the Alpine chamois: the influence of snow–meteorological factors. Ann Glaciol 49:56–62

Joseph LN, Field SA, Wilcox C, Possingham HP (2006) Presence–Absence versus Abundance Data for Monitoring Threatened Species. Conserv Biol 20:1679–1687. doi: 10.1111/j.1523-1739.2006.00529.x

Juillerat L (2005) Extension rapide de l'aire de distribution de Cupido alcetas (Hoffmansegg, 1804) (Lepidoptera, Lycaenidae) en Suisse occidentale en 2003 et 2004. Bull Romand D'entomologie 22:81–95

Jump AS, Mátyás C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol Evol 24:694–701. doi: 10.1016/j.tree.2009.06.007

Kawecki TJ (2008) Adaptation to Marginal Habitats. Annu Rev Ecol Evol Syst 39:321–342. doi: 10.1146/annurev.ecolsys.38.091206.095622

Keller V, Gerber A, Schmid H, et al (2010) Lista Rossa Uccelli nidificanti - Specie minacciate in Svizzera, stato 2010. Ufficio federale dell'ambiente, Berna, e Stazione ornitologica svizzera, Sempach

Kéry M, Royle JA, Schmid H (2005) Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models. Ecol Appl 15:1450–1461. doi: 10.1890/04-1120

Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press

Keßler T, Cierjacks A, Ernst R, Dziock F (2012) Direct and indirect effects of ski run management on alpine Orthoptera. Biodivers Conserv 21:281–296. doi: 10.1007/s10531-011-0184-z

Khare S, Ghosh SK (2016) Satellite Remote Sensing Technologies for Biodiversity Monitoring and Its Conservation. Int J Adv Earth Sci Eng 5:375–389

King R (2012) A review of Bayesian state-space modelling of capture–recapture–recovery data. Interface Focus rsfs20110078. doi: 10.1098/rsfs.2011.0078

Klaus S, Andreev AV, Bergmann H-H, et al (1989) Die Auerhühner. Die Neue Brehm-Bücherei. Westarp Wissenschaften, Magdeburg

Klaus S, Bergmann H-H, Marti C, et al (1990) Die Birkhühner. Die Neue Brehm-Bücherei. Westarp Wissenschaften, Magdeburg

Klebelsberg R (1913) Das Vordringen der Hochgebirgsvegetation in den Tiroler Alpen. Osterreichische Bot Z 63:177–187

Knaus P, Graf R, Guélat J, et al (2011) Historischer Brutvogelatlas: Die Verbreitung der Schweizer Brutvögel seit 1950 = Atlas historique des oiseaux nicheurs ; La répartition des oiseaux nicheurs de Suisse depuis 1950, 1. Aufl. Eigenverl, Sempach

Koch B, Edwards PJ, Blanckenhorn WU, et al (2015) Shrub Encroachment Affects the Diversity of Plants, Butterflies, and Grasshoppers on Two Swiss Subalpine Pastures. Arct Antarct Alp Res 47:345–357. doi: 10.1657/AAAR0013-093

Kormann U, Gugerli F, Ray N, et al (2012) Parsimony-based pedigree analysis and individual-based landscape genetics suggest topography to restrict dispersal and connectivity in the endangered capercaillie. Biol Conserv 152:241–252. doi: 10.1016/j.biocon.2012.04.011

Körner C (2012) Alpine treelines. Springer

Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. J Biogeogr 31:713–732

Körner C, Spehn E (2003) Mountain biodiversity: a global assessment. CRC Press, Basel

Kozlowski G (2008) Is the global conservation status assessment of a threatened taxon a utopia? Biodivers Conserv 17:445–448. doi: 10.1007/s10531-007-9278-z

Kozma R, Melsted P, Magnússon KP, Höglund J (2016) Looking into the past – the reaction of three grouse species to climate change over the last million years using whole genome sequences. Mol Ecol 25:570–580. doi: 10.1111/mec.13496

Kramer-Schadt S, Niedballa J, Pilgrim JD, et al (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. Divers Distrib 19:1366–1379. doi: 10.1111/ddi.12096

Kulakowski D, Bebi P, Rixen C (2011) The interacting effects of land use change, climate change and suppression of natural disturbances on landscape forest structure in the Swiss Alps. Oikos 120:216–225. doi: 10.1111/j.1600-0706.2010.18726.x

Kulakowski D, Rixen C, Bebi P (2006) Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. For Ecol Manag 223:66–74. doi: 10.1016/j.foreco.2005.10.058

Kurki S, Lindén H (1995) Forest Fragmentation Due to Agriculture Affects the Reproductive Success of the Ground-Nesting Black Grouse Tetrao tetrix. Ecography 18:109–113

Kurki S, Nikula A, Helle P, Lindén H (2000) Landscape Fragmentation and Forest Composition Effects on Grouse Breeding Success in Boreal Forests. Ecology 81:1985–1997. doi: 10.1890/0012-9658(2000)081[1985:LFAFCE]2.0.CO;2

Kvasnes MAJ, Storaas T, Pedersen HC, et al (2009) Spatial dynamics of Norwegian tetraonid populations. Ecol Res 25:367–374. doi: 10.1007/s11284-009-0665-7

Laiolo P, Dondero F, Ciliento E, Rolando A (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. J Appl Ecol 41:294–304. doi: 10.1111/j.0021-8901.2004.00893.x

Laiolo P, Rolando A (2005) Forest bird diversity and ski-runs: a case of negative edge effect. Anim Conserv Forum 8:9–16. doi: 10.1017/S1367943004001611

Lampila P, Ranta E, Mönkkönen M, et al (2011) Grouse dynamics and harvesting in Kainuu, northeastern Finland. Oikos 120:1057–1064. doi: 10.1111/j.1600-0706.2010.18788.x

Larcher W, Kainmüller C, Wagner J (2010) Survival types of high mountain plants under extreme temperatures. Flora - Morphol Distrib Funct Ecol Plants 205:3–18. doi: 10.1016/j.flora.2008.12.005

Lawton JH (1993) Range, population abundance and conservation. Trends Ecol Evol 8:409–413

Lebreton J-D (2005) Dynamical and Statistical Models for Exploited Populations. Aust N Z J Stat 47:49–63. doi: 10.1111/j.1467-842X.2005.00371.x

Legagneux P, Blaize C, Latraube F, et al (2009) Variation in home-range size and movements of wintering dabbling ducks. J Ornithol 150:183–193. doi: 10.1007/s10336-008-0333-7

Lehikoinen A, Green M, Husby M, et al (2014) Common montane birds are declining in northern Europe. J Avian Biol 45:3–14. doi: 10.1111/j.1600-048X.2013.00177.x

Lenoir J, Svenning J-C (2015) Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography 38:15–28. doi: 10.1111/ecog.00967

Léonard P (1989) Méthode de dénombrement de tétras-lyre mâles au chant et présentation des résultats

Léonard P (1992) Méthode de dénombrement de Galliformes de montagne en été avec chiens d'arrêt et présentation des résultats

Leonelli G, Pelflni M, Cella UM di, Garavaglia V (2011) Climate Warming and the Recent Treeline Shift in the European Alps: The Role of Geomorphological Factors in High-Altitude Sites. AMBIO J Hum Environ 40:264–273. doi: 10.1007/s13280-010-0096-2

Liberg O, Bergström R, Kindberg J, Von Essen H (2010) Ungulates and their management in Sweden. In: European Ungulates and their Management in the 21st Century. Cambridge University Press, p 604

Lindén H, Helle E, Helle P, Wikman M (1996) Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. Finn Game Res 49:4–11

Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. J Biogeogr 40:778–789. doi: 10.1111/jbi.12058

Liu X, Zhang L, Hong S (2011) Global biodiversity research during 1900–2009: a bibliometric analysis. Biodivers Conserv 20:807–826. doi: 10.1007/s10531-010-9981-z

Loison A, Appolinaire J, Jullien J-M, Dubray D (2006) How reliable are total counts to detect trends in population size of chamois Rupicapra rupicapra and R. pyrenaica? Wildl Biol 12:77–88. doi: 10.2981/0909-6396(2006)12[77:HRATCT]2.0.CO;2

Losinger I, Chautan M, Magnani Y (2011) Pastoralisme et tétras-lyre. Faune Sauvage 291:20–27

Ludwig GX, Alatalo RV, Helle P, et al (2006) Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. Proc R Soc B Biol Sci 273:2009–2016. doi: 10.1098/rspb.2006.3538

Ludwig T, Storch I, Gärtner S (2009a) Large-scale land use change may explain bird species declines in semi-natural areas: the case of Black Grouse population collapse in Lower Saxony, Germany. J Ornithol 150:871–882. doi: 10.1007/s10336-009-0410-6

Ludwig T, Storch I, Graf RF (2009b) Historic landscape change and habitat loss: the case of black grouse in Lower Saxony, Germany. Landsc Ecol 24:533–546. doi: 10.1007/s10980-009-9330-3

Ludwig T, Storch I, Wübbenhorst J (2008) How the Black Grouse was lost: historic reconstruction of its status and distribution in Lower Saxony (Germany). J Ornithol 149:587–596. doi: 10.1007/s10336-008-0306-x

Lüps P (1980) Daten zur Vertikalverbreitung und zum Lebensraum des Steinhuhns Alectoris graeca in den Schweizeralpen. Ornithol Beob 77:209–218

Lüps P (1981) Gedanken zur Besiedlung des Alpenraums durch das Steinhuhn Alectoris graeca. J Fuer Ornithol 122:393–401

Lüps P (2004) Schnee als limitierender Faktor für das Steinhuhn Alectoris graeca in den Schweizer Alpen – eine Übersicht. Ornithol Beob 101:295–306

Luzar JB, Silvius KM, Overman H, et al (2011) Large-scale Environmental Monitoring by Indigenous Peoples. BioScience 61:771–781. doi: 10.1525/bio.2011.61.10.7

Maggini R, Lehmann A, Kéry M, et al (2011) Are Swiss birds tracking climate change?: Detecting elevational shifts using response curve shapes. Ecol Model 222:21–32. doi: 10.1016/j.ecolmodel.2010.09.010

Maggini R, Lehmann A, Zbinden N, et al (2014) Assessing species vulnerability to climate and land use change: the case of the Swiss breeding birds. Divers Distrib 20:708–719. doi: 10.1111/ddi.12207

Magnani Y (1988) Sélection de l'habitat de reproduction et influence de l'évolution des pratiques sylvo-pastorales sur la population de tétras lyre (Tetrao tetrix L.) de la réserve de Frêtes (Haute-Savoie). Gibier Faune Sauvage 5:289–307

Magnani Y (1992) Incidence de l'évolution de pratiques sylvo-pastorales sur le Tétras lyre. Aménage. Nat. 108:33–34

Maillard D, Muffat-Joly B, Constant G, et al (2012) Gestion pastorale et conservation du lagopède alpin : une démarche novatrice. Faune Sauvage 296:4–9

Mardia KV, Jupp PE (1999) Directional statistics. John Wiley & Sons

Marini L, Klimek S, Battisti A (2011) Mitigating the impacts of the decline of traditional farming on mountain landscapes and biodiversity: a case study in the European Alps. Environ Sci Policy 14:258–267. doi: 10.1016/j.envsci.2010.12.003

Marjakangas A (1986) On the winter ecology of the black grouse, Tetrao tetrix, in central Finland. Acta Univ Ouluensis Ser 183 Biol 29:1–87

Marjakangas A, Rintamäki H, Hissa R (1984) Thermal Responses in the Capercaillie Tetrao urogallus and the Black Grouse Lyrurus tetrix Roosting in the Snow. Physiol Zool 57:99–104. doi: 10.1086/physzool.57.1.30155972

Marti C, Bossert A (1985) Beobachtungen zur Sommeraktivität und Brutbiologie des Alpenschneehuhns Lagopus mutus im Aletschgebiet (Wallis). Ornithol Beob 82:153–168

Marti C, Bossert A, Pauli H-R (2016) Bestand und Verbreitung von Birkhuhn Tetrao tetrix und Alpenschneehuhn Lagopus muta im Aletschgebiet von 1970 bis 2015. Ornithol Beob 113:1–30

Martin K, Hannon SJ (1987) Natal philopatry and recruitment of willow ptarmigan in north central and northwestern Canada. Oecologia 71:518–524. doi: 10.1007/BF00379290

Martinoli A, Preatoni DG, Bisi F, et al (2017) Where is the pulse to have the finger on? A retrospective analysis of two decades of Alpine Galliforms (Aves: Galliformes) census and game bag data in Italy. Eur J Wildl Res 63:. doi: 10.1007/s10344-017-1122-5

Marty E, Mossoll-Torres M (2011) Point–count method for estimating rock ptarmigan spring density in the Pyrenean chain. Eur J Wildl Res 58:357–363. doi: 10.1007/s10344-011-0541-y

Mather AS, Fairbairn J (2000) From Floods to Reforestation: The Forest Transition in Switzerland. Environ Hist 6:399–421. doi: 10.3197/096734000129342352

Maunder MN, Punt AE (2013) A review of integrated analysis in fisheries stock assessment. Fish Res 142:61–74. doi: 10.1016/j.fishres.2012.07.025

Mayer AC, Estermann BL, Stöckli V, Kreuzer M (2005) Experimental determination of the effects of cattle stocking density and grazing period on forest regeneration on a subalpine wood pasture. Anim Res 54:153–171. doi: 10.1051/animres:2005018

Mayer AC, Stöckli V (2005) Long-Term Impact of Cattle Grazing on Subalpine Forest Development and Efficiency of Snow Avalanche Protection. Arct Antarct Alp Res 37:521–526. doi: 10.1657/1523-0430(2005)037[0521:LIOCGO]2.0.CO;2

McGarigal K, Ene E (2015) Fragstats: spatial pattern analysis program for categorical maps. Version 4.2. University of Massachusetts, Amherst

McPherson JM, Myers RA (2009) How to infer population trends in sparse data: examples with opportunistic sighting records for great white sharks. Divers Distrib 15:880–890. doi: 10.1111/j.1472-4642.2009.00596.x

Meier R (1998) Sozioökonomische Aspekte von Klimaänderung und Naturkatastrophen in der Schweiz. Hochschulverlag, Zurich, Switzerland

Menéndez R, Megías AG, Hill JK, et al (2006) Species richness changes lag behind climate change. Proc R Soc Lond B Biol Sci 273:1465–1470. doi: 10.1098/rspb.2006.3484

Meriggi A, Pandini V, Sacchi O, et al (1998) Fattori influenzanti la presenza e la dinamica di popolazione della coturnice (Alectoris graeca saxatilis) in Trentino. Rep Cent Ecol Alp 15:5–36

Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evol Appl 7:1–14. doi: 10.1111/eva.12137

Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36:1058–1069. doi: 10.1111/j.1600-0587.2013.07872.x

Meyer R, Millar RB (1999) BUGS in Bayesian stock assessments. Can J Fish Aquat Sci 56:1078–1087. doi: 10.1139/f99-043

Meyer WB, Turner BLI (1994) Changes in Land Use and Land Cover: A Global Perspective. Cambridge University Press, New York

Miner BG, Sultan SE, Morgan SG, et al (2005) Ecological consequences of phenotypic plasticity. Trends Ecol Evol 20:685–692. doi: 10.1016/j.tree.2005.08.002

Moleón M, Almaraz P, Sánchez-Zapata JA (2008) An Emerging Infectious Disease Triggering Large-Scale Hyperpredation. PLOS ONE 3:e2307. doi: 10.1371/journal.pone.0002307

Moleón M, Almaraz P, Sánchez-Zapata JA (2013) Inferring ecological mechanisms from hunting bag data in wildlife management: a reply to Blanco-Aguiar et al. (2012). Eur J Wildl Res 59:599–608. doi: 10.1007/s10344-013-0711-1

Møller AP, Flensted-Jensen E, Mardal W (2006) Rapidly advancing laying date in a seabird and the changing advantage of early reproduction. J Anim Ecol 75:657–665. doi: 10.1111/j.1365-2656.2006.01086.x

Montadert M, Leonard P (2003) Survival in an expanding hazel grouse Bonasa bonasia population in the southeastern French Alps. Wildl Biol 9:357–364

Monteiro AT, Fava F, Hiltbrunner E, et al (2011) Assessment of land cover changes and spatial drivers behind loss of permanent meadows in the lowlands of Italian Alps. Landsc Urban Plan 100:287–294. doi: 10.1016/j.landurbplan.2010.12.015

Morganti M, Preatoni D, Sarà M (2017) Climate determinants of breeding and wintering ranges of lesser kestrels in Italy and predicted impacts of climate change. J Avian Biol n/a-n/a. doi: 10.1111/jav.01179

Moser L, Fonti P, Büntgen U, et al (2010) Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. Tree Physiol 30:225–233. doi: 10.1093/treephys/tpp108

Moss R, Oswald J, Baines D (2001) Climate change and breeding success: decline of the capercaillie in Scotland. J Anim Ecol 70:47–61

Motta R, Morales M, Nola P (2006) Human land-use, forest dynamics and tree growth at the treeline in the Western Italian Alps. Ann For Sci 63:739–747. doi: 10.1051/forest:2006055

Murcia C (1995) Edge effects in fragmented forests: implications for conservation. Trends Ecol Evol 10:58–62. doi: 10.1016/S0169-5347(00)88977-6

Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC (2002) Large-scale habitat variability, delayed density effects and red deer populations in Norway. J Anim Ecol 71:569–580. doi: 10.1046/j.1365-2656.2002.00622.x

Nardelli R, Andreotti A, Bianchi E, et al (2015) Rapporto sull'applicazione della Direttiva 147/2009/CE in Italia: dimensione, distribuzione e trend delle popolazioni di uccelli (2008-2012). ISPRA

Negro M, Isaia M, Palestrini C, et al (2010) The impact of high-altitude ski pistes on ground-dwelling arthropods in the Alps. Biodivers Conserv 19:1853–1870. doi: 10.1007/s10531-010-9808-y

Negro M, Isaia M, Palestrini C, Rolando A (2009) The impact of forest ski-pistes on diversity of ground-dwelling arthropods and small mammals in the Alps. Biodivers Conserv 18:2799–2821. doi: 10.1007/s10531-009-9608-4

Nelli L, Meriggi A, Franzoi A (2013) Habitat selection by breeding rock ptarmigan Lagopus muta helvetica males in the western Italian Alps. Wildl Biol 19:382–389. doi: 10.2981/13-009

Newton I (2013) Bird populations. William Collins

Nichols JD, Conroy MJ, Anderson DR, Burnham KP (1984) Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Trans North Am Wildl AndNatural Resour Conf 49:566–593

Nichols JD, Hines JE, Sauer JR, et al (2000) A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393–408. doi: 10.1642/0004-8038(2000)117[0393:ADOAFE]2.0.CO;2

Nichols JD, Johnson FA, Williams BK (1995) Managing North American waterfowl in the face of uncertainty. Annu Rev Ecol Syst 26:177–199

Nichols JD, Williams BK (2006) Monitoring for conservation. Trends Ecol Evol 21:668–673. doi: 10.1016/j.tree.2006.08.007

Nopp-Mayr U, Zohmann M (2007) Spring densities and calling activities of Rock Ptarmigan (Lagopus muta helvetica) in the Austrian Alps. J Ornithol 149:135–139. doi: 10.1007/s10336-007-0231-4

Novoa C, Astruc G, Desmet J-F, Besnard A (2016) No short-term effects of climate change on the breeding of Rock Ptarmigan in the French Alps and Pyrenees. J Ornithol 1–14. doi: 10.1007/s10336-016-1335-5

Novoa C, Besnard A, Brenot JF, Ellison LN (2008) Effect of weather on the reproductive rate of Rock Ptarmigan Lagopus muta in the eastern Pyrenees. Ibis 150:270–278. doi: 10.1111/j.1474-919X.2007.00771.x

Novoa C, Magnani Y, Auliac P, et al (2002) La restauration des habitats de reproduction de tétras-lyre dans les Alpes du Nord. Faune Sauvage 257:49–54

Nussey DH, Postma E, Gienapp P, Visser ME (2005) Selection on Heritable Phenotypic Plasticity in a Wild Bird Population. Science 310:304–306. doi: 10.1126/science.1117004

Otaki JM, Hiyama A, Iwata M, Kudo T (2010) Phenotypic plasticity in the range-margin population of the lycaenid butterfly Zizeeria maha. BMC Evol Biol 10:252. doi: 10.1186/1471-2148-10-252

Ozenda P (1985) La végétation de la chaîne alpine dans l'espace montagnard européen, Elsevier Masson

Palumbo G, Lo Valvo M (1999) Management Statement - Sicilian Rock Partridge Alectoris graeca whitakeri

Pannekoek J, van Strien AJ (2001) TRIM 3 Manual (TRends and Indices for Monitoring data). Research paper no. 0102. Statistic Netherlands, Voorburg

Parolo G, Rossi G (2008) Upward migration of vascular plants following a climate warming trend in the Alps. Basic Appl Ecol 9:100–107. doi: 10.1016/j.baae.2007.01.005

Patterson TA, Thomas L, Wilcox C, et al (2008) State–space models of individual animal movement. Trends Ecol Evol 23:87–94. doi: 10.1016/j.tree.2007.10.009

Patthey P, Signorell N, Rotelli L, Arlettaz R (2012) Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. Eur J Wildl Res 58:59–70. doi: 10.1007/s10344-011-0540-z

Patthey P, Wirthner S, Signorell N, Arlettaz R (2008) Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. J Appl Ecol 45:1704–1711. doi: 10.1111/j.1365-2664.2008.01547.x

Pauli H, Gottfried M, Reiter K, et al (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA* master site Schrankogel, Tyrol, Austria. Glob Change Biol 13:147–156. doi: 10.1111/j.1365-2486.2006.01282.x

Pauls SU, Nowak C, Bálint M, Pfenninger M (2013) The impact of global climate change on genetic diversity within populations and species. Mol Ecol 22:925–946. doi: 10.1111/mec.12152

Pearce-Higgins JW, Yalden DW, Whittingham MJ (2005) Warmer springs advance the breeding phenology of golden plovers <Emphasis Type="Italic">Pluvialis apricaria</Emphasis> and their prey (Tipulidae). Oecologia 143:470–476. doi: 10.1007/s00442-004-1820-z

Pearman PB, Guisan A, Zimmermann NE (2011) Impacts of climate change on Swiss biodiversity: An indicator taxa approach. Biol Conserv 144:866–875. doi: 10.1016/j.biocon.2010.11.020

Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117. doi: 10.1111/j.1365-2699.2006.01594.x

PECBMS (2009) The State of Europe's Common Birds 2008. CSO/RSPB, Prague, Czech Republic

Pedersen ÅØ, Blanchet M-A, Hörnell-Willebrand M, et al (2013) Rock Ptarmigan (Lagopus muta) breeding habitat use in northern Sweden. J Ornithol 155:195–209. doi: 10.1007/s10336-013-1001-0

Permanent Secretariat of the Alpine Convention (2010) The Alps: people and pressures in the mountains, the facts at a glance : vademecum. Permanent Sekretariat of the Alpine Convention, Innsbruck

Pernollet CA, Korner-Nievergelt F, Jenni L (2015) Regional changes in the elevational distribution of the Alpine Rock Ptarmigan Lagopus muta helvetica in Switzerland. Ibis 157:823–836. doi: 10.1111/ibi.12298

Peronace V, Cecere JG, Gustin M, Rondinini C (2012) Lista Rossa 2011 degli uccelli nidificanti in Italia. Avocetta 36:11–58

Phillips SJ (2008) Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography 31:272–278. doi: 10.1111/j.0906-7590.2008.5378.x

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Pierson J, Bernard-Laurent A, Magnani Y, et al Euclidean distances versus effective pathways: a GIS approach for testing the effects of dispersal constraints on spatial genetic structure of Black grouse (Tetrao tetrix Aves, Tetraoninae) populations

Pinheiro J, Bates D, DebRoy S, et al (2016) nlme: Linear and Nonlinear Mixed Effects Models

Piussi P, Pettenella D (2000) Spontaneous afforestation of fallows in Italy. In: Weber N (ed) EFI Proceedings 35. Freiburg

Plieninger T, Höchtl F, Spek T (2006) Traditional land-use and nature conservation in European rural landscapes. Environ Sci Policy 9:317–321. doi: 10.1016/j.envsci.2006.03.001

Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A (eds). Vienna, Austria, pp 1–10

Pollock KH, Nichols JD, Simons TR, et al (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13:105–119. doi: 10.1002/env.514

Ponce FMJ (1992) Régime et sélection alimentaires des poussins de tétras lyre (Tetrao tetrix) dans les Alpes francaises. Gibier Faune Sauvage 9:27–51

Popescu VD, Artelle KA, Pop MI, et al (2016) Assessing biological realism of wildlife population estimates in data-poor systems. J Appl Ecol 53:1248–1259. doi: 10.1111/1365-2664.12660

Popy S, Bordignon L, Prodon R (2010) A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. J Biogeogr 37:57–67. doi: 10.1111/j.1365-2699.2009.02197.x

Potapov R, Sale R (2014) Grouse of the World. New Holland

Pöysä H, Rintala J, Lehikoinen A, Väisänen RA (2013) The importance of hunting pressure, habitat preference and life history for population trends of breeding waterbirds in Finland. Eur J Wildl Res 59:245–256. doi: 10.1007/s10344-012-0673-8

Pradel R (2005) Multievent: An Extension of Multistate Capture–Recapture Models to Uncertain States. Biometrics 61:442–447. doi: 10.1111/j.1541-0420.2005.00318.x

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proc R Soc B Biol Sci 267:1947–1952. doi: 10.1098/rspb.2000.1234

Putman R, Apollonio M, Andersen R (eds) (2011) Ungulate management in Europe: problems and practices. Cambridge University Press, Cambridge, UK ; New York

QGIS Development team (2017) QuantumGIS 2.18

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, Vienna, Austria

Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. J Biogeogr 41:629–643. doi: 10.1111/jbi.12227

Rae S (2015) Strategic placement of Rock Ptarmigan *Lagopus muta* nests adjacent to boulders. Bird Study 62:185–189. doi: 10.1080/00063657.2015.1006163

Rajala P (1974) The structure and reproduction of Finnish populations of Capercaillie, Tetrao urogullus, and Black Grouse, Lyrurus tetrix, on the basis of late summer census data from 1963-66. Finn Game Res 35:1–51

Randi E, Tabarroni C, Rimondi S, et al (2003) Phylogeography of the rock partridge (Alectoris graeca). Mol Ecol 12:2201–2214. doi: 10.1046/j.1365-294X.2003.01899.x

Ranta E, Lindstrom J, Linden H (1995) Synchrony in Tetraonid Population Dynamics. J Anim Ecol 64:767. doi: 10.2307/5855

Ranta E, Lindström J, Lindén H, Helle P (2008) How reliable are harvesting data for analyses of spatio-temporal population dynamics? Oikos 117:1461–1468. doi: 10.1111/j.0030-1299.2008.16879.x

Rebetez M, Reinhard M (2008) Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. Theor Appl Climatol 91:27–34

Regan HM, Ben-Haim Y, Langford B, et al (2005) Robust decision-making under severe uncertainty for conservation management. Ecol Appl 15:1471–1477

Regione Lombardia, ERSAF (2012) Land cover changes in Lombardy over the last 50 years. Regione Lombardia

Rehnus M, Wehrle M, Palme R (2014) Mountain hares Lepus timidus and tourism: stress events and reactions. J Appl Ecol 51:6–12. doi: 10.1111/1365-2664.12174

Reidy JL, Thompson FR, Bailey JW (2011) Comparison of methods for estimating density of forest songbirds from point counts. J Wildl Manag 75:558–568. doi: 10.1002/jwmg.93

Renwick A, Jansson T, Verburg PH, et al (2013) Policy reform and agricultural land abandonment in the EU. Land Use Policy 30:446–457. doi: 10.1016/j.landusepol.2012.04.005

Revermann R, Schmid H, Zbinden N, et al (2012) Habitat at the mountain tops: how long can Rock Ptarmigan (Lagopus muta helvetica) survive rapid climate change in the Swiss Alps? A multi-scale approach. J Ornithol 153:891–905. doi: 10.1007/s10336-012-0819-1

Reznick DN, Ghalambor CK (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112/113:183–198

Rhodes JR, Ng CF, de Villiers DL, et al (2011) Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. Biol Conserv 144:1081–1088. doi: 10.1016/j.biocon.2010.12.027

Rippa D, Maselli V, Soppelsa O, Fulgione D (2011) The impact of agro-pastoral abandonment on the Rock Partridge Alectoris graeca in the Apennines. Ibis 153:721–734

Rist J, Milner-Gulland EJ, Cowlishaw G, Rowcliffe M (2010) Hunter Reporting of Catch per Unit Effort as a Monitoring Tool in a Bushmeat-Harvesting System. Conserv Biol 24:489–499. doi: 10.1111/j.1523-1739.2010.01470.x

Rixen C, Rolando A (2013) The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments

Roberts JP, Schnell GD (2006) Comparison of survey methods for wintering grassland birds. J Field Ornithol 77:46–60. doi: 10.1111/j.1557-9263.2006.00024.x

Rockström J, Steffen W, Noone K, et al (2009) A safe operating space for humanity. Nature 461:472–475

Rödel HG, Dekker JJA (2012) Influence of weather factors on population dynamics of two lagomorph species based on hunting bag records. Eur J Wildl Res 58:923–932. doi: 10.1007/s10344-012-0635-1

Rogers GE (1963) Blue Grouse Census and Harvest in the United States and Canada. J Wildl Manag 27:579. doi: 10.2307/3798468

Rolando A, Caprio E, Rinaldi E, Ellena I (2007) The impact of high-altitude ski-runs on alpine grassland bird communities. J Appl Ecol 44:210–219. doi: 10.1111/j.1365-2664.2006.01253.x

Romeo C, Wauters LA, Preatoni D, et al (2010) Living on the edge: Space use of Eurasian red squirrels in marginal high-elevation habitat. Acta Oecologica 36:604–610. doi: 10.1016/j.actao.2010.09.005

Rotelli L (2014) I miglioramenti ambientali degli habitat riproduttivi del Fagiano di monte (Tetrao tetrix) sulle Alpi

Royle JA, Kéry M (2007) A Bayesian State-Space Formulation of Dynamic Occupancy Models. Ecology 88:1813–1823. doi: 10.1890/06-0669.1

Royle JA, Nichols JD, Kéry M (2005) Modelling occurrence and abundance of species when detection is imperfect. Oikos 110:353–359

Rózsa J, Strand TM, Montadert M, et al (2016) Effects of a range expansion on adaptive and neutral genetic diversity in dispersal limited Hazel grouse (Bonasa bonasia) in the French Alps. Conserv Genet 17:401–412. doi: 10.1007/s10592-015-0792-3

Sáenz–Arroyo A, Roberts CM, Torre J, Cariño-Olvera M (2005) Using fishers' anecdotes, naturalists' observations and grey literature to reassess marine species at risk: the case of the Gulf grouper in the Gulf of California, Mexico. Fish Fish 6:121–133

Sagarin RD, Gaines SD, Gaylord B (2006) Moving beyond assumptions to understand abundance distributions across the ranges of species. Trends Ecol Evol 21:524–530. doi: 10.1016/j.tree.2006.06.008

Sala OE, Chapin FS, Armesto JJ, et al (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774. doi: 10.1126/science.287.5459.1770

Sandercock BK, Nilsen EB, Brøseth H, Pedersen HC (2011) Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan: Harvest and ptarmigan survival. J Anim Ecol 80:244–258. doi: 10.1111/j.1365-2656.2010.01769.x

Sato CF, Wood JT, Lindenmayer DB (2013) The Effects of Winter Recreation on Alpine and Subalpine Fauna: A Systematic Review and Meta-Analysis. PLOS ONE 8:e64282. doi: 10.1371/journal.pone.0064282

Sattler T, Knaus P, Schmid H, Strebel N (2016) The State of Birds in Switzerland online. Stazione Ornitol. Svizzera Sempach

Sauer JR, Peterjohn BG, Link WA (1994) Observer Differences in the North American Breeding Bird Survey. The Auk 111:50–62. doi: 10.2307/4088504

Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. J Ornithol 152:227–237. doi: 10.1007/s10336-010-0632-7

Schaub M, Gimenez O, Sierro A, Arlettaz R (2007) Use of Integrated Modeling to Enhance Estimates of Population Dynamics Obtained from Limited Data. Conserv Biol 21:945–955. doi: 10.1111/j.1523-1739.2007.00743.x

Scherini GC, Tosi G, Guidali F, Ferrario G (1989) Indagine faunistica sulla consistenza, dinamica di popolazione e gestione venatoria del Gallo forcello (Tetrao tetrix) sulle Alpi lombarde. Regione Lombardia - Settore Agricoltura

Scherini GC, Tosi G, Wauters LA (2003) Social behaviour, reproductive biology and breeding success of alpine Rock ptarmigan Lagopus mutus helveticus in Northern Italy. Ardea 91:11–23

Schipper AM, Koffijberg K, Weperen M van, et al (2011) The distribution of a threatened migratory bird species in a patchy landscape: a multi-scale analysis. Landsc Ecol 26:397–410. doi: 10.1007/s10980-010-9566-y

Schmidt B (2004) Declining amphibian populations: the pitfalls of count data in the study of diversity, distribution, dynamics and demography. Herpetol J 14:167–174

Schmiegelow FKA, Machtans CS, Hannon SJ (1997) Are Boreal Birds Resilient to Forest Fragmentation? An Experimental Study of Short-Term Community Responses. Ecology 78:1914–1932. doi: 10.1890/0012-9658(1997)078[1914:ABBRTF]2.0.CO;2

Schweiger A-K, Nopp-Mayr U, Zohmann M (2012) Small-scale habitat use of black grouse (Tetrao tetrix L.) and rock ptarmigan (Lagopus muta helvetica Thienemann) in the Austrian Alps. Eur J Wildl Res 58:35–45. doi: 10.1007/s10344-011-0537-7

Scoz L, Cavulli F, Fedrigotti A, et al (2016) New data on the first human settlements in western Trentino: The site of Pozza Lavino in the Ledro valley (Trentino, Italy). Quat Int 423:49–57. doi: 10.1016/j.quaint.2015.11.112

Secretariat of the Convention on Biological Diversity (2014) Global Biodiversity Outlook 4. Montreal

Segelbacher G, Piertney S (2007) Phylogeography of the European capercaillie (Tetrao urogallus) and its implications for conservation. J Ornithol 148:269–274. doi: 10.1007/s10336-007-0153-1

Segelbacher G, Storch I (2002) Capercaillie in the Alps: genetic evidence of metapopulation structure and population decline. Mol Ecol 11:1669–1677. doi: 10.1046/j.1365-294X.2002.01565.x

Seiler A, Helldin JO, Seiler C (2004) Road mortality in Swedish mammals: results of a drivers' questionnaire. Wildl Biol 10:225–233

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR (2008) Climate Change, Elevational Range Shifts, and Bird Extinctions. Conserv Biol 22:140–150. doi: 10.1111/j.1523-1739.2007.00852.x

Selås V, Sonerud GA, Framstad E, et al (2011) Climate change in Norway: warm summers limit grouse reproduction. Popul Ecol 53:361–371. doi: 10.1007/s10144-010-0255-0

Sergio F, Pedrini P (2007) Biodiversity gradients in the Alps: the overriding importance of elevation. Biodivers Conserv 16:3243–3254. doi: 10.1007/s10531-006-9113-y

Settele J, Kudrna O, Harpke A, et al (2008) Climatic Risk Atlas of European Butterflies. BioRisk 1:1–712. doi: 10.3897/biorisk.1

Shaffer ML (1981) Minimum Population Sizes for Species Conservation. BioScience 31:131–134. doi: 10.2307/1308256

Signorell N, Wirthner S, Patthey P, et al (2010) Concealment from predators drives foraging habitat selection in brood-rearing Alpine black grouse Tetrao tetrix hens: habitat management implications. Wildl Biol 16:249–257. doi: 10.2981/09-028

Silveira L, Jácomo ATA, Diniz-Filho JAF (2003) Camera trap, line transect census and track surveys: a comparative evaluation. Biol Conserv 114:351–355. doi: 10.1016/S0006-3207(03)00063-6

Soininen EM, Fuglei E, Pedersen ÅØ (2016) Complementary use of density estimates and hunting statistics: different sides of the same story? Eur J Wildl Res 62:151–160. doi: 10.1007/s10344-016-0987-z

Sorace A, Artese C, Antonucci A, et al (2013a) Status and distribution of rock partridge Alectoris graeca in Apennine areas. Avocetta 37:111–118

Sorace A, Guglielmi S, Properzi S, et al (2013b) Rock partridge Alectoris graeca in Lazio region (Central Italy): Status and Action Plan. Avocetta 37:141–144

Sorace A, Properzi S, Guglielmi S, et al (2011) La Coturnice nel Lazio: status e piano d'azione

Soulé ME (1985) What Is Conservation Biology? BioScience 35:727–734. doi: 10.2307/1310054

Soulé ME (1991) Conservation: Tactics for a Constant Crisis. Science 253:744–750

Spanò S, Bocca M (1988) Coturnice (Alectoris graeca). In: Atlante degli uccelli nidificanti in Piemonte e Val d'Aosta 1980-1984. Museo Regionale di Scienze Naturali, Torino

Speakman JR, Król E (2010) Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms: Heat dissipation limit theory. J Anim Ecol no-no. doi: 10.1111/j.1365-2656.2010.01689.x

Stastistik Austria (2017) Jagdstatistik 2016/2017

Stearns SC (1989) The Evolutionary Significance of Phenotypic Plasticity. BioScience 39:436–445. doi: 10.2307/1311135

Storaas T, Kastdalen L, Wegge P (1999) Detection of forest grouse by mammalian predators: A possible explanation for high brood losses in fragmented landscapes. Wildl Biol 5:187–192

Storch I (2000) Status Survey and Conservation Action Plan 2000-2004: Grouse. IUCN

Storch I (ed) (2007) Grouse: status survey and conservation action plan 2006-2010. IUCN ; World Pheasant Assoc., Gland, Switzerland; Fordingbridge, UK

Su YS, Yajima M (2015) R2jags: A Package for Running jags from R. R package version 0.03-08

Südbeck P, Bauer H-G, Boschert M, et al (2007) Rote Liste der Brutvögel Deutschlands - 4. Fassung, 30 November 2007. Berichte Zum Vogelschutz 44:23–81

Sunde P, Overskaug C, Bolstad JP, Øien IJ (2001) Living at the limit: ecology and behaviour of Tawny Owls Strix aluco in a northern edge population in central Norway. Ardea 89:495–508

Sutherland WJ (ed) (2006) Ecological Census Techniques: A Handbook. Cambridge University Press

Svensson SE (1979) Census Efficiency and Number of Visits to a Study Plot when Estimating Bird Densities by the Territory Mapping Method. J Appl Ecol 16:61. doi: 10.2307/2402728

Tasser E, Leitinger G, Tappeiner U (2017) Climate change versus land-use change—What affects the mountain landscapes more? Land Use Policy 60:60–72. doi: 10.1016/j.landusepol.2016.10.019

Tasser E, Tappeiner U (2002) Impact of land use changes on mountain vegetation. Appl Veg Sci 5:173–184. doi: 10.1658/1402-2001(2002)005[0173:IOLUCO]2.0.CO;2

Tasser E, Walde J, Tappeiner U, et al (2007) Land-use changes and natural reforestation in the Eastern Central Alps. Agric Ecosyst Environ 118:115–129. doi: 10.1016/j.agee.2006.05.004

Tavecchia G, Besbeas P, Coulson T, et al (2009) Estimating Population Size and Hidden Demographic Parameters with State-Space Modeling. Am Nat 173:722–733. doi: 10.1086/598499

Temple SA (1986) Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. In: Verner J, Morrison M, Ralph CJ (eds) Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA., pp 301–304

Theurillat J-P (1995) Climate Change and the Alpine Flora: Some Perspectives. In: Guisan A, Holten JI, Spichiger R, Tessier L (eds) Potential Ecological Impacts of Climate Change in the Alps and Fennoscandian Mountains. Conservatoire et Jardin botaniques, Genève, pp 121– 127

Thiel D, Jenni-Eiermann S, Palme R, Jenni L (2011) Winter tourism increases stress hormone levels in the Capercaillie Tetrao urogallus. Ibis 153:122–133. doi: 10.1111/j.1474-919X.2010.01083.x

Thomas CD, Bodsworth EJ, Wilson RJ, et al (2001) Ecological and evolutionary processes at expanding range margins. Nature 411:577–581. doi: 10.1038/35079066

Thomas CD, Cameron A, Green RE, et al (2004) Extinction risk from climate change. Nature 427:145–148

Thomas L (1996) Monitoring Long-Term Population Change: Why are there so Many Analysis Methods? Ecology 77:49–58. doi: 10.2307/2265653

Thompson WL (2002) Towards reliable bird surveys: accounting for individuals present but not detected. The Auk 119:18–25. doi: 10.1642/0004-8038(2002)119[0018:TRBSAF]2.0.CO;2

Thuiller W, Guéguen M, Georges D, et al (2014) Are different facets of plant diversity well protected against climate and land cover changes? A test study in the French Alps. Ecography 37:1254–1266. doi: 10.1111/ecog.00670

Trocchi V, Riga F, Sorace A (2016) Piano d'azione nazionale per la Coturnice (Alectoris graeca)

Ueno M, Solberg EJ, Iijima H, et al (2014) Performance of hunting statistics as spatiotemporal density indices of moose (Alces alces) in Norway. Ecosphere 5:1–20. doi: 10.1890/ES13-00083.1

UICN France, MNHN, LPO, SEOF & ONCFS (2011) La Liste rouge des espèces menacées en France - Chapitre Oiseaux de France métropolitaine. Paris, France.

Unbehaun W, Pröbstl U, Haider W (2008) Trends in winter sport tourism: challenges for the future. Tour Rev 63:36–47. doi: 10.1108/16605370810861035

Valladares F, Matesanz S, Guilhaumon F, et al (2014) The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol Lett 17:1351–1364. doi: 10.1111/ele.12348

van Deventer AP, Ward AD, Gowda PH, Lyon JG (1997) Using Thematic Mapper data to identify contrasting soil plains and tillage practices. Photogramm Eng Remote Sens 63:87–93

VanDerWal J, Shoo LP, Graham C, Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecol Model 220:589–594. doi: 10.1016/j.ecolmodel.2008.11.010

Véran S, Lebreton J-D (2008) The potential of integrated modelling in conservation biology: A case study of the black-footed albatross (Phoebastria nigripes). Can J Stat 36:85–98. doi: 10.1002/cjs.5550360109

Visinoni L, Pernollet CA, Desmet J-F, et al (2014) Microclimate and microhabitat selection by the Alpine Rock Ptarmigan (Lagopus muta helvetica) during summer. J Ornithol 156:407–417. doi: 10.1007/s10336-014-1138-5

Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. Proc R Soc B Biol Sci 275:649–659. doi: 10.1098/rspb.2007.0997

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proc R Soc B Biol Sci 272:2561–2569. doi: 10.1098/rspb.2005.3356

Viterbi R, Imperio S, Alpe D, et al (2015) Climatic control and population dynamics of black grouse (Tetrao tetrix) in the Western Italian Alps. J Wildl Manag 79:156–166. doi: 10.1002/jwmg.810

Vittoz P, Cherix D, Gonseth Y, et al (2013) Climate change impacts on biodiversity in Switzerland: A review. J Nat Conserv 21:154–162. doi: 10.1016/j.jnc.2012.12.002

Vittoz P, Rulence B, Largey T, Freléchoux F (2008) Effects of Climate and Land-Use Change on the Establishment and Growth of Cembran Pine (Pinus cembra L.) over the Altitudinal Treeline Ecotone in the Central Swiss Alps. Arct Antarct Alp Res 40:225–232. doi: 10.1657/1523-0430(06-010)[VITTOZ]2.0.CO;2

Volis S, Mendlinger S, Olsvig-Whittaker L, et al (1998) Phenotypic variation and stress resistance in core and peripheral populations of Hordeum spontaneum. Biodivers Conserv 7:799–813. doi: 10.1023/A:1008844504010

Wallentin G, Tappeiner U, Strobl J, Tasser E (2008) Understanding alpine tree line dynamics: An individual-based model. Ecol Model 218:235–246. doi: 10.1016/j.ecolmodel.2008.07.005

Wallmo OC, Jackson AW, Hailey TL, Carlisle RL (1962) Influence of Rain on the Count of Deer Pellet Groups. J Wildl Manag 26:50–55. doi: 10.2307/3798167

Walther G-R, Beißner S, Burga CA (2005) Trends in the upward shift of alpine plants. J Veg Sci 16:541–548. doi: 10.1111/j.1654-1103.2005.tb02394.x

Wang G, Hobbs NT, Giesen KM, et al (2002) Relationships between climate and population dynamics of white-tailed ptarmigan Lagopus leucurus in Rocky Mountain National Park, Colorado, USA. Clim Res 23:81–87

Warren PK, Baines D (2002) Dispersal, survival and causes of mortality in black grouse Tetrao tetrix in northern England. Wildl Biol 8:91–97

Watkins AF, McWhirter JL, King CM (2010) Variable detectability in long-term population surveys of small mammals. Eur J Wildl Res 56:261–274. doi: 10.1007/s10344-009-0308-x

Watson RT, United Nations Environment Programme (eds) (1995) Global biodiversity assessment: summary for policy-makers. Cambridge University Press, Cambridge [England] ; New York, NY, USA

Wegge P, Kastdalen L (2008) Habitat and diet of young grouse broods: resource partitioning between Capercaillie (Tetrao urogallus) and Black Grouse (Tetrao tetrix) in boreal forests. J Ornithol 149:237–244. doi: 10.1007/s10336-007-0265-7

White GC, Lubow BC (2002) Fitting Population Models to Multiple Sources of Observed Data. J Wildl Manag 66:300–309. doi: 10.2307/3803162

Whitman DW, Agrawal AA (2009) What is phenotypic plasticity and why is it important. In: Whitman DW, Ananthakrishan TN (eds) Phenotypic plasticity of insects: Mechanisms and consequences. NH: Sci. Publ., Enfield, pp 1–63

Wilcove DS, McLellan C, Dobson AP (1986) Habitat fragmentation in the temperate zone. In: Soulé ME (ed) Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts, pp 237–56

Willebrand T, Hörnell-Willebrand M, Asmyhr L (2011) Willow grouse bag size is more sensitive to variation in hunter effort than to variation in willow grouse density. Oikos 120:1667–1673. doi: 10.1111/j.1600-0706.2011.19204.x

Williams BK, Johnson FA, Wilkins K (1996) Uncertainty and the Adaptive Management of Waterfowl Harvests. J Wildl Manag 60:223. doi: 10.2307/3802220

Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press

Wipf S, Rixen C, Fischer M, et al (2005) Effects of ski piste preparation on alpine vegetation. J Appl Ecol 42:306–316. doi: 10.1111/j.1365-2664.2005.01011.x

Wisz MS, Hijmans RJ, Li J, et al (2008) Effects of sample size on the performance of species distribution models. Divers Distrib 14:763–773. doi: 10.1111/j.1472-4642.2008.00482.x

With KA, Crist TO (1995) Critical Thresholds in Species' Responses to Landscape Structure. Ecology 76:2446–2459. doi: 10.2307/2265819

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. Trends Ecol Evol 16:446–453. doi: 10.1016/S0169-5347(01)02205-4

Zbinden N (1987) Zum Aufzuchterfolg des Birkhuhns Tetrao tetrix im Tessin. Ornithol Beob 84:49–61

Zbinden N, Salvioni M (1997) Die Bejagung des Birkhahns im Tessin 1963-1995. Ornithol Beob 94:331–346

Zbinden N, Salvioni M (2003) I gallinacei delle montagne ticinesi

Zbinden N, Salvioni M, Stanga P (2003) La situazione del fagiano di monte Tetrao tetrix nel Cantone Ticino alla fine del ventesimo secolo

Zeileis A, Hothorn T (2002) Diagnostic Checking in Regression Relationships. R News 2:7–10

Zimmermann P, Tasser E, Leitinger G, Tappeiner U (2010) Effects of land-use and land-cover pattern on landscape-scale biodiversity in the European Alps. Agric Ecosyst Environ 139:13–22. doi: 10.1016/j.agee.2010.06.010

Zipkin EF, Saunders SP (2018) Synthesizing multiple data types for biological conservation using integrated population models. Biol Conserv 217:240–250. doi: 10.1016/j.biocon.2017.10.017

Zohmann M, Pennerstorfer J, Nopp-Mayr U (2013) Modelling habitat suitability for alpine rock ptarmigan (Lagopus muta helvetica) combining object-based classification of IKONOS imagery and Habitat Suitability Index modelling. Ecol Model 254:22–32. doi: 10.1016/j.ecolmodel.2013.01.008

Zulka KP (ed) (2005) Rote Listen gefährdeter Tiere Österreichs - Checklisten, Gefährdungsanalysen, Handlungsbedarf. Teil 1: Säugetiere, Vögel, Heuschrecken, Wasserkäfer, Netzflügler, Schnabelfliegen, Tagfalter. Böhlau- Verlag, Wien

Zurell D, Grimm V, Rossmanith E, et al (2012) Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps. Ecography 35:590–603. doi: 10.1111/j.1600-0587.2011.07200.x

Zweifel R, Eugster W, Etzold S, et al (2010) Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. New Phytol 187:819–830. doi: 10.1111/j.1469-8137.2010.03301.x