



**Viability and management of an endangered capercaillie
(*Tetrao urogallus*) metapopulation**

Thèse de doctorat

présentée à la

Faculté des Sciences de
l'Université de Lausanne

Par

Sébastien Sachot

Biologiste diplômé
Université de Lausanne

Jury

Prof. Jacques Boéchat, Président
Prof. Nicolas Perrin, Directeur de thèse
Dr. Cornelis Neet, Expert
Dr. Ilse Storch, Expert

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(Tetrao urogallus) metapopulation**

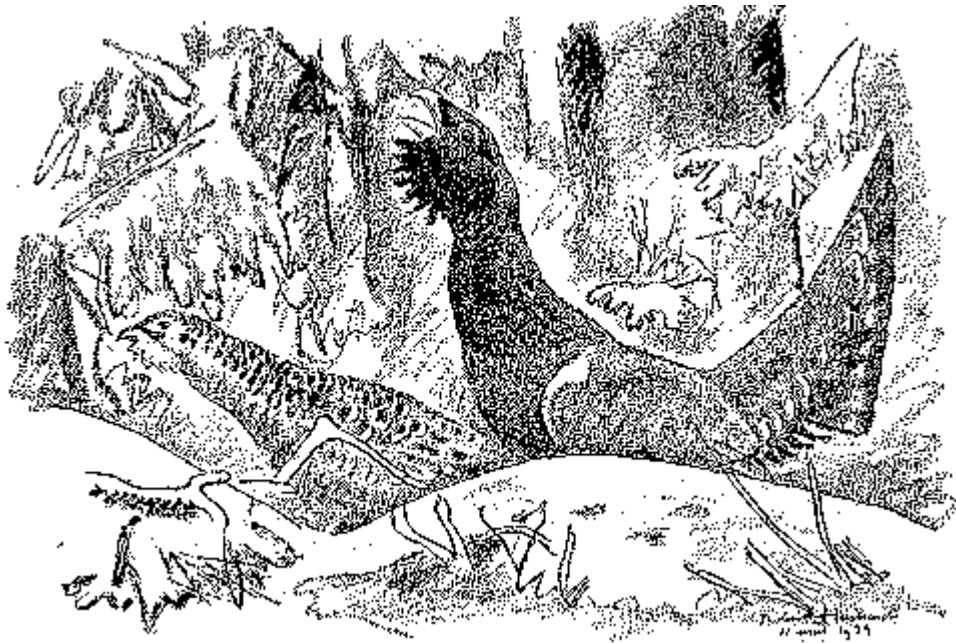
Lausanne, le 22 mars 2002

pour Le Doyen de la Faculté des Sciences



Prof. Jacques Boéchat

To my parents,
To Laurence,
To Nico



Robert Hainard: “Coq et poule”, reproduced with the kind authorization of Pierre Hainard.

ABSTRACT

The populations of capercaillie (*Tetrao urogallus*), the largest European grouse, have seriously declined during the last century over most of their range in western and central Europe. In the Jura mountains (Switzerland and France), the relict metapopulation is now isolated and critically endangered. This thesis aims at providing an insight into capercaillie dynamics and habitat selection at different levels as well as compare alternative management options with new tools and approaches.

Lek counts showed a large reduction of displaying capercaillie from 1991 onwards. As for other european capercaillie metapopulations, the decrease is attributed to habitat loss and fragmentation, human disturbance, rainy conditions during breeding and predation. Nonetheless, life-history sensitive stages and the relative influence of each factor were unknown. Thus, a spatially structured, stochastic population viability software (TetrasPool) was developed from the life-cycle of forest grouses. Simulations predict a marked decline and a significant extinction risk over the next century. Sensitivity analysis point out key life-history parameters: adult survival, as often advocated for long-lived species, but also reproductive success and juvenile survival.

Where and how to manage capercaillie needs therefore to be addressed. We used the Ecological Niche Factor Analysis to predict capercaillie habitat suitability (HS) and rank influential factors at the landscape level from presence signs and topography, land-use and disturbance databases unified into a geographic information system. The largest favorable areas for capercaillie are located around the Mont Sâla and Grand Risoux and represent adequate targets for management. Comparisons of several basic management scenarios reinforced this idea and suggest that carrying capacities of existing patches should be improved over large areas, independently of the source/sink status. Factors increasing capercaillie HS are 1) elevation, 2) moderate canopy cover 3) bilberry cover while factors decreasing HS are 1) meadows, 2) thickets, 3) buildings, 4) farms 5) roads.

At the local level, we quantified winter habitat selection and detected influential factors for capercaillie and hazel grouse, the second endangered forest-grouse in Switzerland, in a cooccurrence area. By the development of local HS models, we palliate the need for objective habitat estimations. Models results confirm previous knowledges such as capercaillie preference for opened forest, low understorey cover and fir presence, as well as hazel grouse preference for dense understorey cover with rowan, willow, beech and spruce. But results also yield surprises, e.g. capercaillie preference for grazed forest but hazel grouse avoidance of it.

Habitat suitability maps and metapopulation viability analysis were finally linked with a new software (Patcher) that allows exploring detailed management scenarios. Comparison of several management scenarios points out an important limitation of modeling. Beyond variables distribution ranges for a study site, extrapolations cannot be performed. It prevents to test efficient management scenario with large conversion of habitat features.

Capercaillie has large habitat requirements. A three-levels management strategy is a necessity that is compatible with hazel grouse presence. At the local level, forest structure and composition, as well as low human disturbance are essential. Group cut of matures trees will allow both species coexistence, while forest road closure will reduce negative effects of human disturbance on habitat quality and capercaillie life-history parameters. At the population level, a mosaic distribution of habitat types and a multi-layered forest structure must be favorised. At the landscape level, forest sizes and distribution determine capercaillie presence. Large forest patch (> 100 ha) conservation and avoidance of new roads and buildings constructions will limit further habitat loss and fragmentation. This management strategy obviates the need of intensive and logistically expensive approaches such as reintroduction and translocation programs.

The methodology and tools developed here are readily expandable to address similar questions in different contexts from conservation biology. The link between habitat suitability and population viability analysis has the potential to provide a valuable, generalized tool for land-managers and conservation biologists.

RESUME

La majorité des métapopulations de grand tétras (*Tetrao urogallus*) d'Europe centrale et occidentale ont régressé au cours du siècle passé. Dans le massif Franco-Suisse du Jura, la métapopulation relictuelle et actuellement isolée et menacée. Ce travail a pour but d'explorer la dynamique des populations de grand tétras, de décrire la sélection de l'habitat à différents niveaux spatiaux et de comparer des options de gestion à l'aide de nouvelles approches.

Les comptages réalisés sur les places de chant attestent d'une forte diminution de l'espèce depuis 1991. Comme pour d'autres métapopulations d'Europe, ce déclin est attribué à la fragmentation et à la perte d'habitat, aux dérangements humains, ainsi qu'aux mauvaises conditions climatiques printanières et à la prédation. Cependant, les traits de vie sensibles et l'importance relative de ces facteurs demeurent inconnus. Ainsi, un logiciel spatialement structuré et stochastique de dynamique des populations (TetrasPool) est construit sur la base du cycle de vie des Tétrionidés. Les simulations prédisent un fort déclin et un risque d'extinction relativement élevé dans les 100 prochaines années. Des analyses de sensibilité mettent en évidence les paramètres cruciaux du cycle vital : la survie adulte, paramètre déjà connu pour d'autres espèces longévives, mais également le succès reproducteur et la survie juvénile.

Déterminer où et comment agir devient alors une question fondamentale. Nous avons utilisé l'analyse écologique de la niche pour établir une carte de qualité d'habitat (HS) pour le grand tétras et classer les facteurs influents au niveau du paysage à partir de signes de présence, de données topographiques, d'utilisation du sol et de dérangement humain géoréférencés. Les plus grandes zones favorables au grand tétras sont situées dans la région du Mont Sâla et du Risoux et représentent des cibles idéales pour la gestion. De surcroît, la comparaison de plusieurs scénarios simples de gestion soutient cette idée et suggère que les capacités de soutien des populations existantes doivent être augmentées sur de vastes surfaces, indépendamment du statut source/puits. Finalement, la HS des populations de grand tétras augmente avec 1) l'altitude 2) un faible recouvrement arboré 3) la présence de myrtilles et elle diminue avec 1) la présence de champs 2) de haies 3) de bâtiments 4) de fermes d'alpage 5) de routes.

Au niveau local, nous avons quantifié la sélection de l'habitat hivernal par le grand tétras et la gélinotte des bois dans une zone de sympatrie. En développant deux modèles de HS locale, nous fournissons un nouvel outil quantitatif et objectif d'estimation de la qualité d'habitat. Les résultats de ces modèles confirment nos connaissances préalables. Le grand tétras préfère les forêts ouvertes avec un faible recouvrement buissonnant et le sapin blanc pour se nourrir. La gélinotte est liée à un fort recouvrement buissonnant ainsi qu'à la présence de sorbier et de saule pour la nourriture, et de petits épicéas pour se dissimuler des prédateurs. Nos résultats comportent également des surprises comme la forte prédilection du grand tétras pour la forêt parcourue et son évitement par la gélinotte des bois.

La carte de qualité d'habitat et l'analyse de dynamique des populations sont finalement liées avec un nouveau logiciel (Patcher), permettant ainsi d'explorer des scénarios de gestion très détaillés. Les simulations confirment que l'ouverture des forêts et la fermeture des routes forestières diminuent le risque d'extinction. Le déplacement des pistes de ski de fond et la mise à ban de la chasse au sanglier dans certains secteurs n'ont que peu d'influence. Les modifications d'habitat apportées par les cyclones augmentent le risque d'extinction.

Le grand tétras a besoin de grands espaces forestiers. Une gestion à trois niveaux est alors nécessaire et compatible avec celle de la gélinotte des bois. Au niveau local, la structure et la composition forestières ainsi qu'un faible dérangement humain sont essentiels. Des coupes par placettes étalées dans le temps permettront aux deux espèces de coexister. La fermeture des routes forestières va réduire les effets du dérangement humain sur la qualité de l'habitat et sur les paramètres du cycle vital du grand tétras. Au niveau de la population, une distribution en

mosaïque des différents types d'habitat et une structure forestière étagée doivent être encouragées. Au niveau du paysage, la taille et la distribution des forêts déterminent la présence du grand tétras. En conservant des forêts d'au minimum 100 ha et en limitant la création de nouvelles routes et bâtiments en forêt, nous ne contribuerons pas davantage à détruire et à fragmenter l'habitat. Cette stratégie de gestion va permettre d'éviter l'utilisation d'approches plus intenses et coûteuses telles que la réintroduction et le déplacement d'oiseaux à partir d'autres métapopulations.

La méthodologie et les outils développés ici sont prêts à être utilisés pour répondre à d'autres questions dans différents domaines de la biologie de la conservation. Le lien entre la qualité de l'habitat et les analyses de viabilité a le potentiel de fournir un outil efficace et généralisable pour les gestionnaires et les biologistes de la conservation.

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1.1. General introduction

Natural populations are not stable over time. Losses through the death or emigration of individuals rarely match gains from the birth or immigration of others (Begon et al., 1990; Hanski et al., 1996). When mortality rate exceeds birth rate, populations will decline. If this trend persists over a period of time long enough that a significant extinction risk results, then conservation biologists and wildlife managers may have a role to play (Burgman et al., 1993).

The complexity of the real world engenders several possible reasons for population decline and quite often, wildlife managers face several alternative solutions to alter the decline (Akçakaya et al., 1995). While some factors are highly predictable (e.g. the number of eggs in a capercaillie nest), others are nearly inaccessible (e.g. environmental fluctuations). Additionally, humans are usually unable to cope with all real world factors and are surprisingly not very acute to estimate risks: they overestimate low risk events but underestimate higher risk events (Burgman et al., 1993). Population viability analysis (PVA) is therefore indispensable to make quantitative assessments on extinction risk.

PVA is an important tool in conservation biology and involve models building to evaluate factors influencing species decline. It also provides insights into how resource management could change parameters influencing extinction probability (Boyce, 1992). Mathematical models are simplifications of the reality as faithful models with detailed data on reproductive behaviour, inbreeding depression, dispersal, seasonal movements, weather influence on vital rates and density dependent predation soon become too large and too complex to cope with (Hanski, 1991). Data are often incomplete or missing for some parameters so that the precision gained on one side is lost on the other because of unavailable parameters estimations. A reliable model should involve a set of equations representing main mechanisms influencing the species in concern with parameters collected locally in the field over several years (Reed et al., 1998).

Models also have some intrinsic weaknesses and have been severely criticized. Beissinger and Westphal (1998) have shown that simplifying assumptions as well as inaccuracy in parameters values may provide questionable results. Nonetheless, the International Union for the Conservation of Nature (IUCN) recognized population viability models as valuable criteria to assess extinction risk and management options efficiency (IUCN, 1994). Present models refinements (e.g. habitat-based population viability) combined with powerful computer calculations make PVA models valuable estimator of population viability (Gaona et al., 1998).

During the modern period of human history, most recorded extinctions occurred on islands (Hanski, 1991). On the continent, large continuous populations have frequently been submitted to increasing human influence. Secondary effects of habitat modifications are habitat loss and fragmentation (Hanski, 1991). Habitat loss is the conversion from suitable to

totally unsuitable habitats where the species no longer occur. This modification is followed by habitat fragmentation, which frequently leads to species abundance reduction and to metapopulation spatial structure (Johnson, 2000; Rolstad, 1991). Metapopulation persistence relies on chance events in balance between some local populations extinction and colonization (Doncaster et al., 1997). The behaviour (i.e. viability and persistence) of a metapopulation is very likely to differ from the behaviour of a single population (Burgman et al., 1993). Numerous species, including grouse species, have a metapopulation structure over part or entire distribution range (Cramp, 1980). How could we assure their persistence while promoting sustainable resources exploitation ? This is the central question addressed in the thesis with detailed investigations on capercaillie populations from Jura Mountains. Relationships between habitat structure for capercaillie and hazel grouse, the two grouse species that occur sympatrically in the Jura Mountains, were also examined in order to promote grouse-adapted forest exploitation and management plans.

1.2. Grouse species

Grouse (order Galliformes ; subfamily Tetraoninae) have Holarctic distribution with 18 species distributed in the north hemisphere (Lucchini et al., 2001). Grouse occur in various ecological niches, from lowland prairie to forests at different stages, up to mountains tops. None of the 18 species is currently recognised as Threatened according to IUCN criteria (IUCN, 1996) but 13 species are included in national Red Data Book of at least one country. In Switzerland, capercaillie (*Tetrao urogallus*), hazel grouse (*Bonasa bonasia*), black grouse (*Tetrao tetrix*) and rock ptarmigan (*Lagopus lagopus*) are the four native species but only capercaillie and hazel grouse are listed in the Red Data Book (Zbinden et al., 1994).

Adult grouse are sedentary and have some special adaptations to cold climates (Storch, 1993b). Morphological adaptations include feathered feet or small levels on their border to allow movement on the snow, doubled feather to increase birds isolation and a long intestine with caeca to maximize digestion efficiency of poor nutritional items (Couturier, 1964). Energy expenditure is also behaviourally limited during winter, birds having a reduced activity (Gjerde and Wegge, 1989; Swenson and Olsson, 1991). Finally, a shift in feeding behaviour is observed for species in habitats with long snow cover (Leclercq, 1987a). By contrast with summer season where forest grouse mainly feed on ericaceous and herbaceous ground vegetation, during winter, they are mostly arboreal and feed in trees (Jacob, 1988).

1.2.1. The capercaillie

The capercaillie is the largest of all grouse with a pronounced size dimorphism between sexes (Figure 1.1, Table 1.1). Males weight up to 5 kg and are twice heavier than females (Cramp, 1980). It is strictly associated to old-grown or boreal forests, with highly specific habitat requirements in terms of structure and composition (Leclercq, 1987a; Magnani, 1987; Picozzi et al., 1992; Rolstad, 1988; Storch, 1993a). Bilberry (*Vaccinium myrtillus*) represents the major part of its summer diet, while white fir (*Abies alba*) in central Europe, and forest pine (*Pinus silvestris*) in the boreal zone, are required as winter food. Home range varies from 100 to 1000 ha (Gjerde and Wegge, 1989; Leclercq, 1987a; Ménoni, 1991) according to local conditions. These characteristics, together with its high sensitivity to human perturbations (especially during the winter period and the reproductive season), make capercaillie an indicator of undisturbed forest ecosystems (Storch, 1993a).

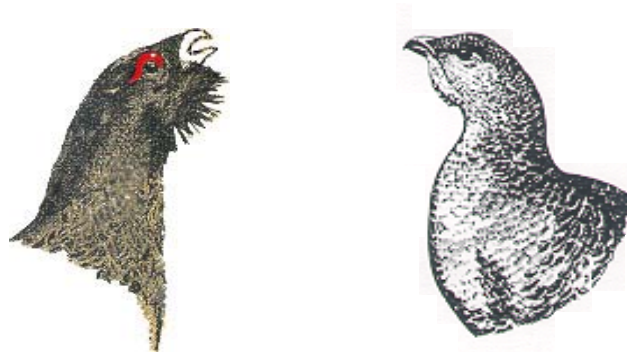


Figure 1.1. Capercaillie male (left) and female (right), (Müller, 1974).

During spring, males display on traditional leks (Cramp, 1980). Males are polygynous and females have an opportunity to operate mate choice on the lek (Table 1.1). After fecundation, females retreated and build nest in a shallow depression on the floor with a few pieces of grass or needles. Mean clutch size is about 8.0 ± 2.0 (SD) eggs (Leclercq, 1981). There is one brood per year but a replacement clutch could occur. Incubation lasts 26 days and is accomplished by the female only. Chicks are precocial and nidifugeous and females' care for them until autumn. Young birds are full grown after three months and become independent soon after. Dispersal occurs in late autumn or early winter. Males are mostly philopatric with short distance dispersal ($\bar{X} = 0.9$ km; $SD = 0.3$) while juvenile females could disperse up to 25 km ($\bar{X} = 8.0$ km; $SD = 2.0$) (Gjerde and Wegge, 1989). Sexual maturity is attained at the end of the first year of life for females and after 3 years for males (Cramp, 1980).

Table 1.1. Comparative biology of capercaillie and hazel grouse.

Parameter	Capercaillie	Hazel grouse
Weight	Males: up to 5 kg, females: 2.5 kg ^a	0.4 kg ^a
Mating system	Leks, polygynous males ^a	Territories, monogamous males ^a
Number of eggs	8 ± 2 ^b	9.4 ± 1.2 ^h
Home range	50-1000 ha ^c	20-60 ha ^{h, i}
Dispersal	Males: 0.9 ± 0.3 km; Females: 8.0 ± 2.0 km ^d	1.2 ± 0.3 km ^h
Local habitat	Old successional stage, opened forest ^e	Young successional stages, dense understory cover ^{h, i}
Summer food	Mainly bilberry and ericaceous shrubs ^e	Numerous plants of the herbaceous layer ⁱ
Winter food	White fir, pine ^{e, f}	Deciduous trees: sorb, rowan, willow ⁱ
Threats	Habitat loss and fragmentation, rainy conditions during breeding, predation ^{e, g}	Habitat loss and fragmentation, predation ^{h, i}
Disturbance	High sensitivity ^{b, e, f}	Low sensitivity ⁱ

^a From Cramp (1980).

^b From Leclercq (1987a and unpublished datas).

^c Home range from Bavarian Alps and Pyrenees (Storch 1993a, Ménoni 1991).

^d Medium value from Sweden and Finland (Wegge et al 1981 ; Koivisto 1963).

^e From Bavarian Alps (Storch 1993a).

^f From Pyrenees (Ménoni 1991).

^g From Scotland (Moss 1986).

^h From Sweden (Swenson 1991, Aberg, 2000).

ⁱ From France (Desbrosses 1997, Montadert 1996).

Many bird species linked to forest late successional stages are particularly endangered (Tucker and Heath, 1994). Capercaillie is no exception. Although the species occupies most of its original range (extending from western Europe to Scandinavia and eastern Siberia), important declines have been documented over the last decades, due to habitat loss,

deterioration and fragmentation, as well as to human disturbance (Ménoni and Bougerol, 1993; Ménoni et al., 1994; Storch, 1994). To a lesser extent, rainy conditions during egg incubation and young rearing, as well as predation (Moss, 1986) locally amplify population decline.

Most western and central European populations, restricted to mountain regions, are isolated and fragmented (Blair et al., 1997). Capercaillie is extinct from Belgium and from low elevation sites in Germany, France and Switzerland (Catusse et al., 1992; Marti, 1987; Müller and Wagner, 1989; Scherzinger, 1987). Over the last 20 years, abundance regression between 40 to 90 % was recorded for most European populations, except in Spain, Romanian and Fennoscandia where capercaillie number seems stable (Blair et al., 1997).

In Switzerland, capercaillie distribution showed a drastic reduction of 20.6 % between 1972-1976 and 1993-1996 (Schifferli et al., 1980; Schmid et al., 1998). Populations in the Bas-Valais, Préalpes Vaudoises and Oberland Bernois are now extinct. The Jura Mountains, Schwytz and Grison Alps are the only Swiss demes with more than 100 birds (Schmid et al., 1998). In France, distribution reduction was also recorded for all metapopulations between 1964 and 1992 (Catusse et al., 1992; Couturier, 1964; Office National de la Chasse, 1977). The Vosges metapopulation shrank from 95 % in 28 years (Ménoni, 1994a) while the Jura metapopulation has a 87 % reduction and the Pyrenees a 5 % reduction of distribution. The French Alps metapopulation is now extinct (Ménoni, comm. pers.).

In the Jura Mountains, capercaillie distribution partly covers Switzerland and France. As a result of cattle farming and silvicultural practices started as early as the 14th century, the distribution of capercaillie has long been patchy (Leclercq, 1987b). It has, however drastically regressed since the 1960s, being now restricted to altitude 1200 m and above (up to 1550 m) (Ménoni, 1994b). The remaining metapopulation is distributed over 35 populations, 24 of which in France (Montadert and Chamouton, 1997) and 11 in Switzerland (Dändliker et al., 1993), covering 542 km² in total. Metapopulation size is estimated at about 500 reproductive birds (Montadert and Chamouton, 1997).

1.2.2. The hazel grouse

Hazel grouse is the smallest European grouse and both sexes weight around 0.4 kg (Cramp, 1980; Figure 1.2, Table 1.1). Hazel grouse has the narrowest requirements for habitat structure among forest grouse in Europe (Swenson and Angelstam, 1993). It requires a dense coniferous cover, primarily spruce and fir with a high degree of canopy closure, a dense coniferous understory and a supply of deciduous trees for catkins and buds as winter food (Desbrosses, 1997; Swenson, 1991). These characteristics implicate that hazel grouse could occur in many different forests physiognomy. Primarily hazel grouse habitat is spruce forest with old-grown structure where wind or snow damage opened small gaps that are colonized by sorb, maple and young spruce (Swenson, 1991). Secondary habitats result from early successional stages after forest exploitation (Desbrosses, 1997).

Hazel grouse is sedentary, mainly monogamous with males that perform a solitary display. Both sexes defend territories between 20-60 ha throughout the year (Montadert, 1996). After mating, female lay 9.4 ± 1.2 (SD) eggs on the ground within a nest constituted of leaves and needles (Cramp, 1980). Female has a unique brood per year but a replacement clutch is possible if the first clutch failed. Males neither contribute to incubation nor to chicks rearing.

Females incubate for 25 days, chicks leave nest soon after hatching (in June within Jura Mts). Chicks are full-grown after 40 days and independent after three months. Juveniles leave their natal home range from late autumn to early spring and realize short distance dispersal for both sexes ($\bar{X} = 1.2$; $SE = 0.3$)(Swenson, 1991). Sexual maturity is achieved after the first year of life.



Figure 1.2. Hazel grouse female (left) and male (right), (ONC, 1997).

Hazel grouse has an extensive range throughout the Palearctic boreal zone extending to central Europe (Bergmann et al., 1982). The subspecies *rupestris* is restricted to central Europe and has the smallest and more fragmented distribution range of the four hazel grouse subspecies (Cramp, 1980). As for capercaillie, habitat loss, habitat fragmentation and predation are major factors driving hazel grouse decline (Aberg, 1996; Swenson, 1993).

Western and central European populations but also Scandinavia and eastern European populations tend to decline in numbers and distribution (Bergmann et al., 1982; Blair et al., 1997). This trend has resulted in the eastward retreat of the western distribution limit. In central Europe, remaining populations are small (< 200 birds) and probably isolated (Storch, 2000).

In Switzerland, hazel grouse distribution only shrinks by 2.6 % between 1972-1976 and 1993-1996 (Schifferli et al., 1980; Schmid et al., 1998). However, hazel grouse has disappeared from the lowland areas of the Plateau and from a few areas in the Jura and in the Prealps while some recently occupied areas were discovered in the Prealps and Alps. The largest demes are located in the Jura Mts, in the Prealps and Alps between 1000-1600 m (Schmid et al., 1998). Estimations of metapopulations sizes are unavailable because this bird is highly secretive and notoriously difficult to census (Desbrosses, 1987; Huboux et al., 1994). In France, hazel grouse distribution has regressed by 40 % between 1964 and 1988 (Bernard-Laurent and Magnani, 1994; Couturier, 1964). Now, the bird has essentially a mountainous distribution but several regressing populations subsist at low altitudes on the north-east Plateaux (Bernard-Laurent and Magnani, 1994). Since 1964, some populations went extinct (e.g. Bugey, Haute-Marne, low Vosges) but the species also have colonized new habitats in alpine regions (e.g. Ventoux, Verdon, Haute-Provence; Bernard-Laurent and Magnani, 1994).

In the Jura Mts, old forest with patchy rejuvenation and young forest with an irregular structure are the commonest habitat types (Desbrosses, 1997). Recent silvicultural practices include selective cutting and group cutting of mature trees and pre-commercial thinning with

shrubs removal. Abandon of intense young beech exploitation from 1960 onwards is an additional factor that contributed to hazel grouse extinction in most populations at low altitudes (< 1000 m) during the last 40 years. Remaining populations are patchily distributed between 1000-1550 m (Montadert and Chamouton, 1997). Mean local abundance of hazel grouse calculated over 10 years was 2.08 ± 3.21 (SD) adults for 100 ha of optimal Jura habitats with annual variation between 0.94 - 3.21 birds for 100 ha forest (Leclercq, 1987c).

1.3. Study area

The Jura Mountains (lat. 47°25' N ; long. 6°42' E), at the border between France and Switzerland, spread over 250 km length and 65 km width at the largest point. Main study area is in Switzerland (Figure 1.1). Landscape is characterized by a succession of forests, pastures, rocky crests and valleys never exceeding 3 km width. Elevation ranges from 500-1677 m and treeline is around 1550 m. Climate is rude with a mean annual temperature of 5.5 °C and an average of 180 frost days per year at 1100 m. Mean annual rainfall is 2000 mm, with 4 m of total snowfall. Snow cover is present from November to May and reaches 0.5-2 m in January. Springs and summers are mild and damp with a growing period that does not exceed four months. Timber harvest occurs in all forests but slow tree grow prevent intensive silvicultural practices such as clearcut and trees are preferentially selectively cut. Human density is low (50-100 people km⁻²) although the area is frequently visited for various types of leisure activities. The main economic activity, cattle farming, occurs in pastures and valleys bottoms.

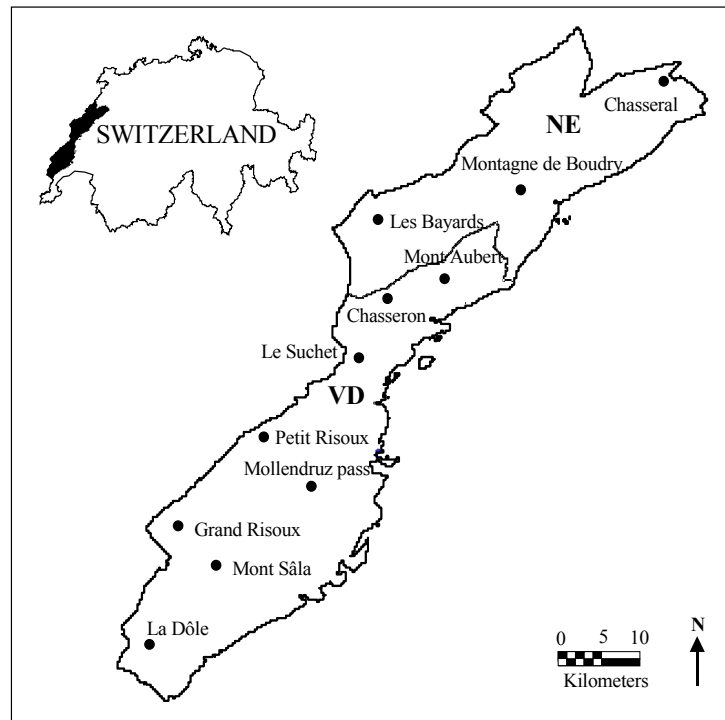


Figure 1.1. Main study area in the Swiss Jura Mountains. Dots indicate principal capercaillie forests. VD: canton de Vaud, NE: Canton de Neuchâtel.

Coniferous forests are dominant from elevation above 1000 m and are mainly represented by the Fir-Beech mountainous association (*Abieti albae-Fagetum sylvaticae typicum*)(Vittoz,

1998). Forests are dominated by spruce (*Picea excelsa*) mixed with beech (*Fagus sylvatica*) and fir. Others deciduous species present in low proportion are maple (*Acer pseudoplatanus*), rowan (*Sorbus aucuparia*), sorb (*Sorbus aria*), dwarf-medlar whitebeam (*Sorbus chamaemespilus*), elder (*Sambucus nigra*), alpine rose (*Rosa pendulina*), fly honeysuckle (*Lonicera* sp.) and hazel (*Corylus avellana*). Willow (*Salix caprea*) is present in damp depressions while laburnum (*Laburnum alpinum*) occurs mainly in southern slopes. Bilberry grows preferentially on acid and poor nutritional grounds with water flush.

Potential predators of adult grouse are goshawk (*Accipiter gentilis*), eagle owl (*Bubo bubo*), red fox (*Vulpes vulpes*) and pine marten (*Martes martes*). Clutches and broods could be destroyed by wild boar (*Sus scrofa*), red fox, pine marten, badger (*Meles meles*), weasel (*Mustela nivalis*), red squirrel (*Sciurus vulgaris*), European jay (*Garrulus glandarius*) and corvids (*Corvus* sp.). Birds of prey are fully protected in Switzerland and France while mammalian predators and corvids are irregularly killed by hunters.

1.4. General methods

1.4.1. Lek count

Capercaillie males display on leks. Territory establishment begin at the end of winter (February-March) and from mid-April to mid-May, all displaying males are present on leks early in the morning (Storch, 1993a). Males are extremely site tenacious and display on the same lek all their life (Wegge and Rolstad, 1986). Yearling and two-years old males are nonterritorial and may visit several leks during the breeding season (Wegge and Rolstad, 1986). These young males may explore up to 15 leks (Ménoni, unpublished data) and then establish a definitive territory in their third year, usually close to their natal range (Wegge and Larsen, 1987). Access to female on the lek is restricted to a few dominant males. Females come several day to choose their mate, copulate once and then fly away from the lek.

Counts were made during this mating period on every known lek of the Jura Mts. There, lek observations are submitted to special authorization from wildlife rangers. Hides must be set before 19:00 p.m. and removed the next morning at least one hour after the last sign of bird presence. One hide is used for leks with less than three birds and two hides for leks with more than three birds. To get reliable results, a minimum of two counts is performed on each lek (Leclercq, 1987a). Between 1991 – 1999, the number of counts per lek varies between two and eight for a lek, as weather and observer availability annually vary. But even years with a low numbers of hide-days, the overall lek area of every lek have been censused. The results of every hide-day are reported on a formulary, gathered by the Groupe Tétrás Jura (France) and the wildlife rangers of the canton de Vaud (Switzerland). The maximum number of males heard or seen during all counts at a lek was retained for analyses. Hens abundance recorded at leks was not used because some hens could visited up to three leks before mating (Storch, 1997).

1.4.2. Route census

Demographic parameters estimations were issued from route census performed in the Risoux population from 1976-2000, between 15-30 July, i.e. one month after hatching (Leclercq, 1987a, and unpublished). A line of 3-8 persons disposed at 25 m interval walked simultaneously through entire forest patches and counted flushed grouse (Leclercq, 1987c).

Birds are sexed and the number of chicks per brood is determined. Age or sex-undetermined birds were omitted for demographical parameters calculations. Sex ratio, adults and juveniles survival rates and proportion of reproductive females were calculated from these field datas. More details on calculations could be found in Leclercq (1987a; 1987c).

1.4.3. Grouse signs

Fieldwork was conducted from 1995 to 2000. All forest plots within the south-western part of the study area (canton de Vaud ; Figure 1.1) were randomly prospected for presence signs (direct sightings, tracks, droppings and feathers). Winter investigations (241 km line transects in 1998-99, and 303 km in 1999-2000) were performed from December to February, 10 days after fresh snowfall to get sufficient detection. Grouse presence was assessed by searching for winter droppings, which have $10.4 \text{ mm} \pm 0.9$ (SD) radius for males capercaillie, $8.1 \text{ mm} \pm 0.6$ (SD) for females while hazel grouse droppings have $6 \text{ mm} \pm 0.5$ (SD) radius for both sexes (Jacob, 1987). To avoid sex misclassification dropping diameters in overlapping distribution area were not attributed to a sex category. Summer signs (mostly droppings and feathers) were searched from June to August of 1995, 1996 and 1998. The variable shape of droppings during the snow free season does not allow sex distinction (Jacob, 1987). My own database was completed with additional indices reported by wildlife rangers over the same time period. Signs were located at $\pm 10 \text{ m}$ in the field (using compass, altimeter, and GPS), then digitalized on a vectorial map, from which a raster layer was finally computed and usable to build habitat suitability maps. All data were pooled over years for analyses, to damp possible variations stemming from weather conditions or population density.

1.4.4. Geographic information system processing

GIS is a computer system for managing spatial data as maps, digital images and georeferenced data. GIS are mainly used to organize data from various sources into a unified database as a serie of data layers, which overlap at each location.

The link between data collected in the real world and GIS techniques is achieved by models. Real world data are coded and represented as either vector or raster models. Vector models are adequate for linear structure, (e.g. roads, altitudes) representations. Points are depicted as a pair of coordinates, lines as series of points and areas as series of lines. This model is ideal for basic mapping such as visualisation but is rather complex to handle when calculations over several layers are involved.

Raster models allow affordable calculations over layers. Each layer refers to a specific attribute, (e.g. altitude, exposure, percentage canopy cover) represented by a serie of grid cells equivalent to computer pixels, with a constant size and usually a square form. Resolution is the real pixel size on the ground. Points are represented as pixels and lines as series of connected pixels. A raster layer is a rectangular matrix of numbers so that row and column numbers addresses cells locations. Coordinates are not stored because they could be derived from the storage order. Total rows, columns numbers and geographic origin location are stored for each layer. GIS datas were analysed with Mapinfo Professional (Mapinfo Corp.), Idrisi32 (Clarks Lab.) and Biomapper (Hirzel et al., in press). Non-spatial statistics were performed on S-Plus (Mathsoft Inc.).

1.4.5. Programming

Programming of informatic modules strongly reduces time expense for repetitive operations (e.g. PVA simulations, GIS data formatting and spatial analyses) and furnishes valuable tools for land-managers and scientists. Thus, I conceived and realized several modules : TetrasPool, Patcher, OmitColumn, InterventionFinder. These programs were written in Pascal with an object-oriented mode (Delphi 4, Inprise Corp.). TetrasPool is the core program of the thesis and include a spatially structured population viability analysis with a user-friendly interface. For further details on TetrasPool, refer to Chapters 2 & 3 and Appendix 1.

Patcher determines patch or population structures from habitat suitability maps. This module allow to link landscape data, i.e. a habitat suitability map, with demographic data via TetrasPool. Patcher output files are in Idrisi32 format and in text format with x and y centroid coordinates and carrying capacities for every population. More details on Patcher are available at Chapter 7.

The last two modules are utilities. Theirs functionalities and fields of application are briefly described here. OmitColumn was built to extract rapidly a few columns from a two-dimensional array with numerous columns. It is only after columns extractions that land-use and vegetation datas could be integrated into a vectorial GIS. I used this program to extract land-use datas (Geostat database) obtained from the Swiss Federal Office of Statistics and species from a vegetation database (Atlas Phyto-Vaud) developed by the Service Forêts-Faune-Nature.

InterventionFinder was written to simultaneously add and substract specific GIS maps on several GIS layers. The map calculator on Idrisi32 performs the same task but for one map only and the process is slow. These drawbacks are avoided in InterventionFinder because many maps could be combined at the same time. I used this module to combine maps and build management scenarios.

1.5. Aims and thesis contents

My main objectives are 1) to provide an insight into capercaillie dynamics and habitat selection at different levels 2) to provide land-managers a useful tool to assess grouse population viability within a spatially structured landscape 3) to compare alternative management options and their relative impact on population persistence. Hazel grouse habitat selection is also locally examined as this species occurs sympatrically within capercaillie distribution range in the Jura Mountains.

The thesis is organized on six main Chapters with Chapters 2-7 dealing with abundance trends, population viability analysis, habitat selection and management strategies. In Chapter 2, main trends of capercaillie abundance were inspected from lek counts. In Chapter 3, I develop a spatially structured, stochastic, metapopulation viability model for capercaillie, usable for any species with similar life-history traits. I applied this model to the Jura Mts capercaillie metapopulation in Chapter 4. To promote grouse-adapted silviculture, winter habitat selection was then inspected at the local level for capercaillie and sympatric hazel grouse in order to detect local requirements of species (Chapter 5). In Chapter 6, I investigated habitat suitability for capercaillie at the landscape level : is capercaillie occurrence predictable from topographical, land-use and human disturbance features ? In Chapter 7, I present a GIS

linked-population viability analysis for capercaillie within a human-induced landscape and rank management strategies.

Parts of this thesis have been presented in the following papers :

S. Sachot, B. Leclercq and M. Montadert (in press). Population trends of capercaillie (*Tetrao urogallus*) in the Jura Mountains between 1991 and 1999. *Game & Wildlife Science*.

S. Sachot, N. Perrin and C. Neet. (in press). Winter habitat selection by two sympatric forest grouse in western Switzerland: implication for conservation. *Biological Conservation*.

S. Sachot, N. Perrin and C. Neet. (submitted). Viability and management of an endangered Capercaillie population in the Jura Mountains.

K. Fattebert, S. Sachot, N. Perrin and C. Neet. (submitted). Evaluation of capercaillie *Tetrao urogallus* habitat in the Jura Mountains (western Switzerland).

S. Sachot, N. Perrin and C. Neet. (submitted). Habitat suitability analysis for capercaillie (*Tetrao urogallus*) in the Swiss Jura Mountains.

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2.1. Abstract

1. In several European countries, capercaillie populations have seriously declined in both distribution and abundance during the last decades. Abundance trends of the Jura Mountains metapopulation have not been recently examined.
2. I evaluated changes in the metapopulation of capercaillie between 1991 and 1999, by counting the number of singing males each spring in a sample of 28 leks belonging to seven distinct populations, four in France (in the Doubs and Jura departments) and three in Switzerland (in the Vaud Canton). There were 0 to 13 singing males per lek. In 1999, the subpopulations of two leks were extinct and ten of the leks contained only one male each.
3. There was a significant decrease in the number of males in the metapopulation ($P < 0.001$). The number of males decreased in five of the populations, remained stable in one and increased in the other, which contained only one lek. The most pronounced decline was 9.6 % per year and the increase was 3.5 % per year.
4. The capercaillie abundances varied significantly as a function of year ($P < 0.001$) and population ($P < 0.001$).
5. The decline in the number of males recorded resulted from the combined effects of several factors, and the strengths of these effects differed between populations. I identified the following negative factors in the Jura Mountains: too high a degree of habitat fragmentation, modification of the habitat resulting in closing in of the environment (e.g. invasion of the forest understory by beech), excessive human disturbance, poor weather conditions in spring and high levels of predation. All these factors reduce the reproductive success and survival rate of individual birds, and therefore affect the size of populations.

3.2. Introduction

Variation of species abundance is a major topic in ecology. Animal and plants populations could experience various issues from increase, to stability and even to decrease (Hanski, 1994; Hanski et al., 1995; Watson et al., 1994). These states are rarely stable over time and could occur through the species life cycle, habitat modifications, presence of competitors, predators or parasites (Akçakaya and Altwood, 1997; Christie, 1994; Hastings, 1996; Lahaye et al., 1994; Léonard, 1995; Lindström and Kokko, 1997; Sloan et al., 1998). Abundance variation arises through changes in reproductive success, survival rate or dispersal rate.

In most central and west European populations, capercaillie is now restricted to forests in mountainous regions. Large abundance reduction has occurred in all populations with a few exceptions (Blair et al., 1997). In the Jura Mountains, capercaillie trends were dissimilar between two populations for the 1976-1985 period (Leclercq, 1987a). He noticed a slight decrease followed by a large increase in one population; meanwhile a second population faces a constant and moderate decline.

This chapter will address the following questions: 1) Have the population trends observed until 1991 in the Jura since continued ? 2) Were the population trends similar for all populations or did some populations display different trends ? To answer these questions, we counted the number of males in some leks in the Jura Mountains of Switzerland and France between 1991 and 1999.

2.3. Material and methods

2.3.1. Data collection

Between 1991 and 1999, singing males were counted in spring in the 51 known leks in the Jura Mountains. However, due to inadequate counting (absence of counting in certain years or counting for too short a period) for 23 leks, I included only the 28 leks that were regularly observed. These 28 leks, corresponding to seven different populations (Figure 2.1). The French populations in the Jura and the Doubs (n° 1, 2, 3 and 4) were localised with the aid of a distribution map established in 1991 (Magnani et al., 1991) and the Swiss populations in the Vaud Canton (n° 5, 6 and 7) were localised with the aid of a distribution map established in 1993 (Ecotec Environnement SA, 1993). The geographical position of the leks had not changed between 1991 and 1999. Extra counts were carried out in spring in a 2 km radius around the known leks to confirm the absence of other leks.

2.3.2. Statistical analyses

The analyses were carried out on the maximum number of males recorded per lek and per year (and not on the mean number observed per year). To ensure that the variables were normally distributed, as required for the tests used, the variable *number of males* was transformed into Log (*number of males* +1). Linear regression (Sokal and Rohlf, 1995) was used to detect and to describe the changes in the sizes of the metapopulation (by combining the results from all of the leks studied) and of each individual population (by combining the results for all of the leks in each population). Residuals normality was checked by the Kolmogorov-Smirnov test (Zar, 1984). The annual rate of increase was calculated by $\exp^{(Slope)} - 1$ (Harris, 1986).

I checked that the variances of the populations were homogeneous by the F_{\max} test (Hartley, 1950). I then used analysis of covariance (ANCOVA, Sokal and Rohlf, 1995) to test the effect of the covariable *Year* and the factor *Population* on the variable $\text{Log}(\text{number of males} + 1)$. The normality of the residual was assessed by the Lilliefors test, which is a modified version of the Kolmogorov-Smirnov test (Zar, 1984).

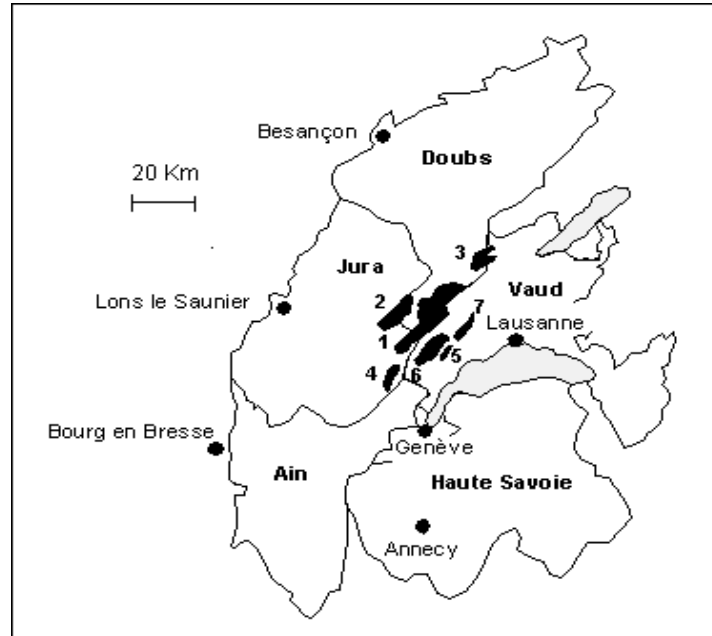


Figure 2.1. Location of the seven populations of capercaillie studied in the Jura Mountains. The French populations in the Doubs and Jura departments (n° 1, 2, 3 and 4) were located using a distribution map established in 1991 (Magnani et al., 1991) and the Swiss populations in the Vaud Canton (n° 5, 6 and 7) were located using a distribution map established in 1993 (Ecotec Environnement SA, 1993).

2.4. Results

The number of male capercaillie present in the spring varied from year to year between 1991 and 1999 (Table 2.1). The overall trend for all of the populations of Jura was a decrease in the number of males ($P < 0.001$; Figure 2.2). In 1999, the subpopulations of the two leks of population n° 2 died out and the subpopulations of ten other leks only contained a single male (Table 2.1).

Changes in abundance differed according to the population (Figure 2.3). The slopes of the regression lines of $\text{Log}(\text{number of males} + 1)$ against *Year* variable were significantly different from 0 ($P_s < 0.01$) for six of the seven populations ($P = 0.498$ for population n° 4; Table 2.2). The number of males was therefore stable in population n° 4. The negative regression slopes for populations n° 1, 2, 5, 6 and 7 indicate that the number of males had decreased, whereas the positive slope for population n° 3 indicated that the number of males had increased. The residuals of all of the linear regressions were normally distributed (Kolmogorov-Smirnov test, $P_s < 0.05$).

Table 2.1. Capercaillie trends on 28 leks within seven populations censused in the Jura Mts between 1991-1999.

Population	Lek	1991	1992	1993	1994	1995	1996	1997	1998	1999
1	1	9	10	10	10	10	10	6	5	5
1	2	5	5	3	4	3	3	3	3	3
1	3	4	3	3	4	3	4	2	1	0
1	4	8	6	5	6	4	0	4	4	3
1	5	4	4	4	5	5	2	1	1	1
1	6	7	5	1	3	6	6	4	6	6
1	7	13	8	9	8	5	4	3	2	2
1	8	3	4	3	2	3	4	3	2	2
1	9	3	6	5	4	6	4	2	3	1
1	10	4	3	3	3	2	2	2	2	1
<i>N</i> ^a		60	54	46	49	47	39	30	29	24
2	1	5	5	4	4	5	2	2	0	0
<i>N</i>		5	5	4	4	5	2	2	0	0
3	1	2	2	2	2	2	2	3	4	4
<i>N</i>		2	2	2	2	2	2	3	4	4
4	1	3	3	7	6	6	0	0 ^b	5	3
4	2	4	5	7	6	6	3	0 ^b	5	3
<i>N</i>		7	8	14	12	12	3	0 ^b	9	6
5	1	2	2	3	3	2	1	1	1	1
5	2	4	2	3	1	1	1	1	1	1
5	3	3	3	1	1	1	1	1	1	1
5	4	3	1	0	1	1	1	1	1	1
<i>N</i>		12	8	7	6	5	4	4	4	4
6	1	6	6	4	4	4	4	3	3	2
6	2	5	5	5	5	4	3	3	2	2
6	3	5	5	5	6	5	5	5	3	1
6	4	6	6	6	7	6	4	4	5	5
6	5	4	4	3	4	5	4	2	1	1
6	6	6	6	6	5	5	4	2	1	1
6	7	6	6	6	5	5	2	5	4	4
<i>N</i>		38	38	35	36	34	26	24	19	16
7	1	2	2	4	4	3	2	2	2	2
7	2	6	6	5	5	4	3	3	4	4
7	3	5	4	3	3	3	2	3	3	3
<i>N</i>		13	12	12	12	10	7	8	9	9
Total N ^c		139	129	122	123	117	85	74	79	67

^a Total abundance for the population.

^b No census on this lek during spring. This value has not been included in the analyses.

^c Total abundance for all populations.

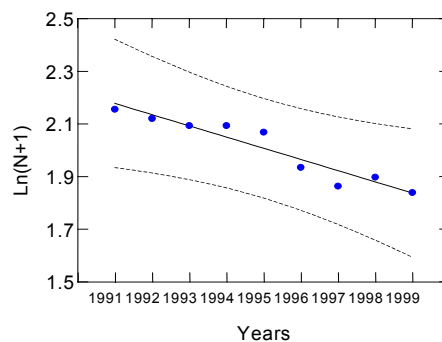


Figure 2.2. Annual changes in the number of male capercaillie counted in spring, between 1991 and 1999, in a sample of 28 leks corresponding to seven populations in the Jura Mountains ($y = 86.925 - 0.043x$; $R^2 = 0.908$, $p < 0.001$). Full line : regression line ; dotted line : 95 % confidence interval.

The mean annual rate of increase was lowest for population n° 2 (9.6 %) and highest for population n° 3 (3.5 % ; Table 2.2).

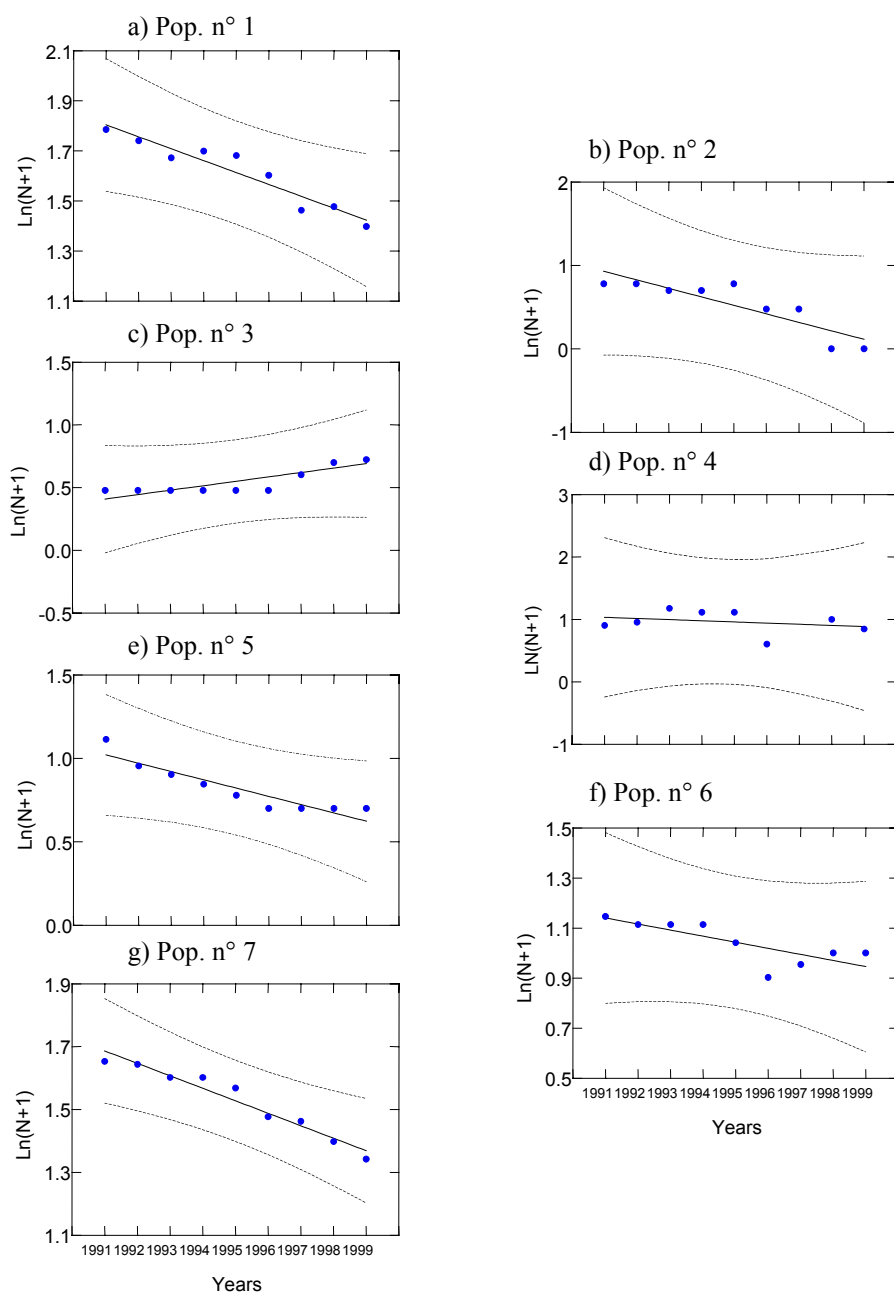


Figure 2.3. Annual changes in the number of male capercaillie counted in spring from 1991 to 1999, in a sample of 28 leks corresponding to seven populations in the Jura Mountains. Number of leks per population: n° 1: 10; n° 2: 1; n° 3: 1; n° 4: 2; n° 5: 4; n° 6: 7; n° 7: 3. Linear regressions are significant for all populations ($P_s < 0.01$). Full line : regression line ; dotted line : 95 % confidence interval. The regression parameters are in Table 2.2. In 1997, population n° 4 was not counted, therefore abundance data is lacking in 1997 for this focal population.

Table 2.2. Annual trends of displaying capercaillie abundance for seven Jura populations between 1991-1999, where $y = \text{Constant} + \text{Slope} \cdot x$. Annual variation is given by $\exp^{(\text{Slope})} - 1$.

Population (n°)	Constant	Slope	Annual variation [%]	R^2	F-ratio	P
1	96.562	-0.048	-4.68	0.912	72.807	<0.001
2	203.765	-0.102	-9.69	0.770	23.471	0.002
3	-69.926	0.035	3.56	0.688	15.442	0.006
4	38.042	-0.019	-1.88	0.080	0.521	0.498
5	99.909	-0.050	-4.87	0.859	42.681	<0.001
6	80.794	-0.040	-3.92	0.949	129.550	<0.001
7	49.475	-0.024	-2.37	0.622	11.499	0.012
1 to 7	86.925	-0.043	-4.20	0.908	69.1	<0.001

As variances were homogeneous for all populations ($F_{\max} = 18.746$, n.s.), I was able to perform an analysis of covariance. I found that there was a “year” effect ($F = 52.226$, $P < 0.001$) and a “population” effect ($F = 20.088$, $P < 0.001$) on capercaillie abundances. The residuals were normally distributed ($n = 63$, Lilliefors test, $P > 0.05$).

2.5. Discussion

2.5.1. Abundance trends

I observed a significant overall decrease in the number of male capercaillie in the leks sampled. These results can probably be extended to the whole of the Jura Mountains, because the sample of leks studied is probably representative of all the leks in this area. Indeed, two pseudorandom processes were used to select the leks, based on the availability of observers and the meteorological conditions. Furthermore, the sample analyzed included more than half (55 %) of the known leks in the Jura. Most of the leks that were not included in the sample contained only small numbers of males during the survey period and belonged to small populations composed of only one or two leks, situated close to larger populations that were sampled. Although not negligible, their contribution to the dynamics of the species is probably very limited. (see: Chapter 4).

Capercaillie populations in the Jura followed three trends: decrease, stability and increase. The decrease observed in population n° 1 has already been in progress for some time. Leclercq (1987a) reported a strong decrease in the number of males and in the reproduction rate in part of this population between 1976 and 1983. During this period, demographic data collected were incompatible with the long-term survival of the population. However, the number of males did increase, returning to 1976 levels within a few years (1985-1992).

As in the Jura, the size of the Vosges metapopulation decreased between 1983 and 1997 (decrease in the total number of males present at 24 singing sites, Palanque, 1999). As in the Jura, different trends in the number of males were recorded in the eight areas containing the leks: three contained populations in decline, four areas had populations that were initially stable and then declined, and one population was stable.

2.5.2. Limiting factors and causes of the decline

Habitat

The presence of the capercaillie depends on the availability and distribution of its suitable habitats (Storch, 1993a). Capercaillie requires opened and layered forest structures, sufficiently quiet and of sufficient size, with adequate food availability in both summer and winter (Leclercq, 1987b; Rolstad et al., 1988; Storch, 1993d). At the landscape level, the distribution of capercaillie in the Jura corresponds to that of mixed beech-fir forest (*Abieti albae-Fagetum sylvaticae typicum*) (Vittoz, 1998). At the sub-population level centered on a lek, the availability of suitable habitats in a 1 km radius determines the number of displaying males (Rolstad and Wegge, 1987b).

The forests of the Jura are heterogeneous (Vittoz, 1998) and suitable habitats for capercaillie are patchily distributed (see: Chapter 6). Each fragment of suitable habitat is included in a matrix of lower quality habitats. In this context, dispersers will only settle if the mean size of the suitable habitats mosaic is between 50-500 ha (Rolstad and Wegge, 1987b; Storch, 1993c). If a mosaic does not satisfy the spatial requirements of the species, the area will not be inhabited on a lasting basis (Rolstad and Wegge, 1987a).

Capercaillie is sensitive to canopy and understory cover: a habitat that is covered by new growth and regeneration for more than 40 % of its surface is unfavourable (Leclercq, 1981). The problem of the closing of the understory by deciduous trees, especially beech, is currently very worrying in the Jura Mountains. The decreasing exploitation of beech and the favourable climate over a succession of years have led to the resettlement and maintenance of high proportions of beech at many high-altitude stations. As a result, forest clearings, which are essential for successful breeding, have been lost following the closure of the understory by young beech trees. Similarly, traditional summer sites have been abandoned by the capercaillie due to increases in the density of the understory. Finally, the high covering of the forest floor by beech prevents the growth of plant species that act as essential sources of food for the capercaillie, such as bilberry in the summer (Jacob, 1988 ; Storch, 1993b) and fir in the winter (Jacob, 1988). This suggests that habitat quality of population n° 4 remained good, thanks notably to fallen trees, which opens up the environment, allowing the population to remain stable. Conversely, the quality of many of the forest sectors containing population n° 1 degraded due to the closure of the understory, leading to a decrease in population size.

According to the principle of habitat selection, the birds should leave unsuitable habitat for more suitable habitat, which may explain the decrease in the number of capercaillie in the leks sampled in the Jura. Such movements have never before been observed in the Jura Mts. This is not surprising because adult males are sedentary and philopatric (Larsen et al., 1981; Rolstad et al., 1998). An adult male is very unlikely to abandon a lek in favour of another one that is already occupied, or to found a new lek with other males (Catusse, 1993; Leclercq, 1987a).

Disturbance

The increase in the number of access roads (forestry road densities around 5.76 km / 100 ha in the Jura Mts), the clearance of snow from these roads in winter and the popularity of off-piste and cross-country skiing are all recent sources of disturbance that have a negative effect on the occupation of habitats and the survival rate of capercaillie in the Jura Mountains.

Disturbance could modify survival rate or reproductive success (Storch, 1993c). Leclercq (1985) showed that disturbances due to forest roads have considerably reduced the size of capercaillie habitats at Grand Risoux and, as a result, the carrying capacity. In the Pyrenees, repeated winter disturbances to the sectors inhabited by the capercaillie have led to a major decrease in their numbers (Ménoni, 1994). The lack of recruitment of young birds in regularly disturbed sectors may account for the observed decline.

Reproductive success

Reproductive success, in addition to adult survival, is a key element in the maintenance of population size for animals with long lifespan, such as the capercaillie. Thus, the low level of reproductive success recorded in population n° 1 over the last 25 years (Leclercq et al., 1997) is worrying. The low level of reproduction observed in population n° 1 was not caused by an increase in the mortality of the chicks because the brood sizes observed in August 1991 to 1999 did not decrease. However, the proportion of females with broods varies considerably from year to year (0.25 ± 0.2 % (SD); Leclercq, 1987c) and is largely conditioned by weather fluctuations and at a smaller extent by predation during eggs incubation and early chick life (Moss, 1986; Moss and Oswald, 1985; Moss et al., 2001). Average reproductive years, such as 1995 (36 % of females had broods, $n = 11$), are often followed by catastrophic years without any reproduction and then by a new period of reproduction, such as 1998 (40 % of females had broods, $n = 5$) and August 1999 (12 %, $n = 8$; B. Leclercq, unpublished data).

Predation

Predation of capercaillie nests and chicks has been described by several authors. Ménoni (1991) found that the frequency of nest predation was 55 % ($n = 9$) in the Pyrenees and Storch (1993c) reported a frequency of nest predation of 29 % ($n = 14$) in the Bavarian Alps. Chicks were exposed to a high level of mortality 62 % ($n = 56$) during the first two weeks after hatching in the Bavarian Alps, and between the second week and second month after hatching in the Pyrenees (49 %, $n = 17$). In these two regions, the contribution of predation to these deaths could not be dissociated from that of climatic conditions. Rainfall has been shown to have an effect on mortality rate in the first two weeks after hatching in Scotland (Moss and Oswald, 1985; Moss et al., 2001).

Nest predation has never been quantified in the Jura Mountains. However, in the sector occupied by population n° 1, Leclercq et al. (1997) observed a strong positive correlation between the abundance of water voles (*Arvicola terrestris*) and the average number of young capercaillie per hen. The potential generalist predators of capercaillie, such as the red fox and the pine marten, tend to eat small mammals rather than alternative prey such as capercaillie during periods in which small mammals are at high densities. The converse is true during phases of small mammal population decline.

Movements and dispersal

The spatial distribution of capercaillie metapopulations is highly fragmented in central Europe (Catusse et al., 1992; Groupe Tétrás Vosges, 1995; Storch, 1993a). The closest metapopulations to those of the Jura are in the Vosges (100 km), central Switzerland (160 km), and Black forest (250 km). The mean dispersal distance for juvenile is between 990 m (SE = 270 m) (Gjerde and Wegge, 1989) and 6700 m (SE = 1100 m) (Swenson, 1991) in the boreal zone and data for central Europe have similar ranges (Ménoni, unpublished data;

Storch, 1993c). A maximum dispersion distance of 75 km has been observed in the boreal zone (Myrberget, 1978). Distances separating the various metapopulations are clearly larger than the known dispersal capacities of the species. Therefore, the Jura metapopulation may be considered to be isolated and its dynamics is probably independent of other metapopulations.

2.6. Conclusions

A large reduction of displaying capercaillie males was recorded on censused leks between 1991-1999. However, one population increased slightly and another remained stable. Therefore, the trends differ according to the population.

Several factors may influence population decline, the strength of their effects differing according to site. In the Jura Mountains, the decrease in population size can be attributed to habitat fragmentation and modification (principally understory closure by beech), human disturbances, poor weather conditions in spring and predation. These factors directly affect the reproductive success of the species and the survival rates of juveniles and adults.

Counting singing males on leks provides a reliable estimation of the abundance trends of capercaillie populations, although juveniles (aged below three years) and very old males (aged over 15 years) do not sing on the leks (Leclercq, 1987a). My analyses were carried out over a relatively short period of time (1991-1999); I recommend the counting of capercaillie for the next decade to confirm my results. Annual counts regularity is essential. Leks with missing data could not be included in statistical analyses and I omit 45 % of all censused leks for this reason. In the future, efforts should be made to achieve counts uninterruptedly on as many leks as possible. More observers are needed or efforts should be focused on restricted subset of leks, representative of the Jura metapopulation.

The counting of singing males in leks is a first step towards understanding the demography of capercaillie. Other informations are necessary to determine the relative effects of the possible causes of population decline and to identify the sensitive parameters in the life cycle, in order to focus management options adequately.

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TetrasPool, a spatially explicit model to assess population viability

3

3.1. Abstract

1. A new model to assess the viability of spatially structured population, TetrasPool, is developed from the life cycle of forest grouse. TetrasPool is a stochastic population model where populations initially have similar life-history parameters with parameter variations issued from both environmental and demographic stochasticity. Variations between populations could extent from perfect synchrony to entire asynchrony with a user specified correlation factor among patches.
2. The model is based on the female sex. Adults are philopatric while juveniles (less than 1 year old) could disperse between populations. Dispersal events accounts for the spatial structure of populations. The probability to reach the target patch is a function of the size, distance, and species abilities to travel long routes. Two dispersal modes are implemented and account for 1) possible species perception of habitat types away from their initial habitats or 2) for the absence of distinction of habitat types outside their range.
3. Among TetrasPool outputs, populations and metapopulation extinction probability as well as median time to extinction are important issues. A dispersal chart allows identifying potential source-sink populations.
4. Sensitivity analysis is a fundamental part of PVA process. TetrasPool can automatically calculate the sensitivity of most life-history parameters.
5. The whole process allows predicting the future of populations, exploring species sensitivity to key life-history parameter and could be used to rank management options.

3.2. Introduction

PVA is a widely used tool to classify numerous threats to species and project population size and persistence over years (Akçakaya and Burgman, 1995; Bro et al., 2000; Bustamante, 1996; Gaona et al., 1998; Wiegand et al., 1998). It also makes intuition explicit because it addresses conservation in a quantitative manner with estimations of extinction probabilities based on species life-history parameters (Brook et al., 1997). This methodology presents a useful and influential planning tool (Clark et al., 1991). Although PVA has the great advantage to introduce a quantitative element into risk assessment, it also has several assumptions and limitations, as any quantitative approaches in ecology (Reed et al., 1998).

Crucial point is the conversion of real-world complex interactions into a functional model. The trade-off between complexity and functionality depends on the characteristics of the species in concern, on the availability of data and on the question addressed (Burgman et al., 1993). Simple models are easy to understand and convenient for several species analysis but they lack realism while being based on simplist assumptions. More sophisticated models are realistic but contain highly detailed informations on the species. The trade-off explains the diversity of spatially structured populations models developed in recent years (Akçakaya, 1994; Akçakaya and Ferson, 1998; Lacy et al., 1995; Legendre and Clobert, 1995; Possingham, 1995). However, when detailed life-history parameters and financial resources are available, it is recommended to construct a model adapted to the species in focus (Burgman et al., 1993; Lindenmayer et al., 1993). In that way, species life-history parameters could be conveniently integrated and restrictive assumptions and limitations of canned-PVA packages are relaxed.

The purpose of this chapter is to present TetrasPool (Sachot, 2000), a new, practical and user-friendly software for PVA conceived on the capercaillie life cycle. Mains assumptions, model strengths and weaknesses are described. Details on software specific procedures and algorithms are also illustrated.

3.3. Model description

3.3.1. Life-cycle

TetrasPool was specifically conceived and developed on the annual life cycle of a forest bird, the capercaillie. The model is convenient for every species with one reproductive period and late summer or autumn juvenile dispersal. Other grouse species, e.g. hazel grouse, black grouse and rock ptarmigan perfectly fit model assumptions. Plants or animals with similar life-history patterns also suit the model.

In TetrasPool, the metapopulation consists in a number of patches, with similar life-history parameters, notwithstanding environmental and demographic stochasticity. The model accounts for the limiting female sex, while it is assumed that males are not a limiting factor. Individuals are assigned to two ages class, juveniles and adults, with different survivorships. Juveniles are less than one year old, could potentially disperse but not reproduce (Ménoni, 1996). By contrast, adults are more than a year old, sedentary and able to reproduce once a year (Catusse, 1988; Wegge and Rolstad, 1986).

The life cycle is similar for each population, with differences between them due to local parameters values. A life cycle represents one year in reality (Figure 3.1). The cycle starts with an initial number of females at time (t), specified for each patch at the onset of the breeding season. Of these, some do not reproduce, either because they do not attempt breeding, or because of total clutch or brood failure. In capercaillie, offspring dispersal occurs in autumn and early winter, apparently at little cost, if any (Wegge and Larsen, 1987). By contrast, winter mortality is heavy, especially on yearlings (Gjerde and Wegge, 1989; Lindén, 1981). The total number of females at time (t + 1) is the sum of juveniles and adults who succeeded in surviving winter.

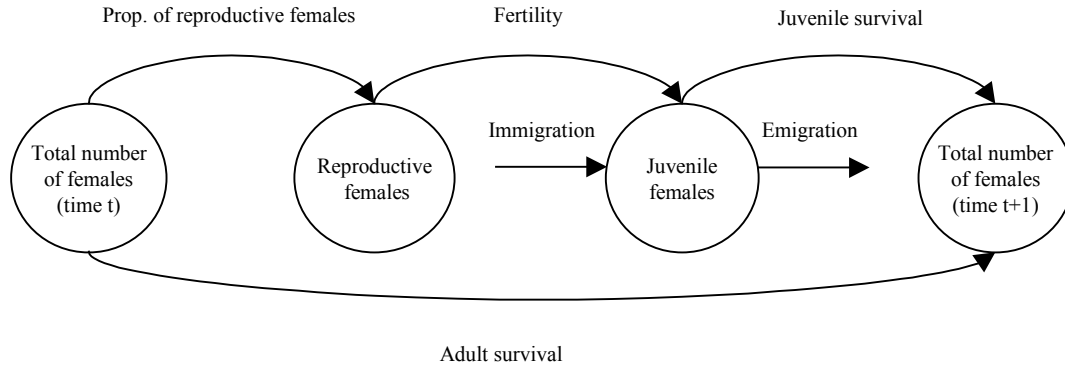


Figure 3.1. Annual life cycle for a population in TetrasPool. The cycle starts at the onset of the breeding season.

3.3.2. Dispersal

TetrasPool is a spatially explicit population model combining PVA with spatial structure of populations (i.e. metapopulation structure). The probability that a dispersing individual reaches a given patch is a function of the size of the target patch, as well as distance from the source patch. For each emigrant, the probability of a successful dispersal from the initial population i to the target population j is characterized as follow :

$$P_{ij} = \arctan[(R_j/D_{ij})] \times 1/\pi \times e^{(-D_{ij}/D_m)} \quad (1)$$

Where R_j is the radius of the target population, D_{ij} the distance between the two centroids of the concerned populations, D_m the average dispersal distance for a juvenile female. Two large and close populations have greater probabilities to exchange dispersers than small and far ones. Due to the negative exponential, the probability to reach population j decreases as distance between populations increases.

Two dispersal modes are implemented in TetrasPool. First, the « Random direction » mode assumes a radial dispersal from the initial population center to every direction. Individuals, which do not encounter another population while dispersing, are assumed dead. Second, the « Directional dispersion » mode assumes that emigrants always reach others populations and are not getting lost in the matrix of unsuitable habitats. The target population that receives an emigrant is defined in the following way: dispersal probabilities are standardized so that their sum equals unity with:

$$p_{ij} = P_{ij} / \sum_{i \neq l} P_{il} \quad (2)$$

Where P_{il} is the dispersal probability from population i to population l . Then a random number is drawn from a uniform distribution [0,1] and compared to p_{ij} . If the random number

is smaller than p_{ij} , then an emigrant is assigned to population j . When the random number is larger to p_{ij} , final probability is calculated as the sum of p_{ij} and $p_{i(j+1)}$ and compared to the random number. This process is repeated until the random number is inferior to the sum of standardized probabilities. Then, an emigrant is assigned to the population who lastly contributed to be larger to the random number. This procedure is repeated until all emigrants have been assigned to a target population.

3.3.3. Carrying capacity and density dependence

Carrying capacity represents the population size that environmental resources can just carry without a tendency to either increase or decrease (Begon et al., 1990). In TetrasPool, the carrying capacity for local populations is defined as the maximum number of territories available for breeding hens within a forest patch. The precise form of density dependence in natural capercaillie populations is actually unknown, but unlikely to be of crucial importance in the present instance, as the focal population drastically declined over the recent years and is thus presumably largely below saturation. Therefore I chose a ceiling type of density dependence, the number of adult females on each patch being limited by the local carrying capacity, itself a function of patch surface (maximum number of breeding territories). If the number of adults exceeds carrying capacity at the end of a timestep, individuals are randomly removed from the population, independently of the age class, until abundance is equal to the carrying capacity.

3.3.4. Stochasticity

Deterministic models do not incorporate any variance in parameters values. Populations will grow or decrease in a deterministic way, depending on life-history parameters. By the way, strong populations trends are detected but models are unrealistic because there are always random variations in natural populations dynamics. Demographic variation, environmental variation, spatial variation and genetic variation are the four major sources of random fluctuations that could affect population dynamics and viability (Schaffer, 1981). Accurate informations on genetic variation are lacking for most rare species. Therefore, TetrasPool includes demographic stochasticity, environmental stochasticity and spatial variation with correlation among environmental variations.

Demographic stochasticity is introduced by attributing individual status (i.e. whether the focal individual survives or not, reproduces or not, disperses or not) from a binomial sampling, and individual fecundity from a Poisson sampling. Demographic variance exists because real populations are discrete, structured and often quite small (Burgman et al., 1993). It reflects the fact that at each time step, each juvenile of a population could disperse or not and adults can breed or not, survive or die, have a big clutch or a smaller one.

Environmental stochasticity accounts for the unpredictable influence of environment, like weather, on some vital rates. For example, environmental stochasticity in the proportion of reproductive females incorporate that entire capercaillie clutches and broods may be lost due to wet weather. Environmental stochasticity is introduced by sampling the proportion of reproductive females, juvenile survival rate, adult survival rates, dispersal rate and fecundity from Beta samplings. This patch-specific value of parameters has mean and standard deviation defined for the whole metapopulation.

The spatial structure of environmental noise is known to matter: asynchrony between populations diminish extinction risk by averaging out fluctuations caused by demographic or environmental stochasticity (Boyce, 1992; Lahaye et al., 1994). Accordingly, TetrasPool, correlation affects the proportion of females with chicks, because weather fluctuations are known to affect brood failure in capercaillie (Moss et al., 2001), and they do show spatial correlation.

Environmental correlation is modeled with two samplings from Beta distributions, which allow correlation to vary from 0 to 1 among patches. The aim is to generate partially correlated values for the proportion of reproductive females. Total variance is split into a between-years component (*Sigma*) and a within-years, among-population component (*Epsilon*). Sigma value is thus defined as the part of the standard deviation in the proportion of reproductive females, which varies among years, but is common to all populations within years:

$$Sigma = Psd \times (Pvr/100) \quad (3)$$

Where *Psd* is the standard deviation of the proportion of reproductive females parameter and *Pvr* the percentage of variance shared between populations. When *Sigma*=1, populations are completely correlated; at the opposite, when *Sigma*=0, populations are totally uncorrelated. Epsilon is the complement of Sigma:

$$Epsilon = Psd - Sigma \quad (4)$$

For each time step, a value is first sampled for the whole metapopulation from a Beta sampling, with a mean equal to the proportion-of-reproductive-females parameter, and a standard deviation equal to sigma. Then, this value is used as mean, and epsilon as standard deviation, for a second sampling from a Beta sampling, the latter being repeated for each population. As a result, the among-population correlation in the proportion of reproductive females will increase with sigma. If percentage of variance shared between populations is equal to 100, then sigma equals the standard deviation in the proportion of reproductive females, so that all populations within one year have the same value for this parameter.

3.3.5. Model outputs

Among the results provided by TetrasPool (Table 3.1), extinction probabilities and median time to extinction are important issues. Extinction probability refers to the proportion of extinctions recorded for all replicates at the end of simulations. At the end of all simulations, median time to extinction is calculated for extinct runs. Median time to extinction is calculated rather than mean extinction time, the latter being largely influenced by fortunate runs. Extinction time distribution is generally very skewed on the right tail of the distribution, i.e. a large proportion of populations goes extinct at a much larger time than average.

Table 3.1. TetrasPool outputs, abbreviations and units. - : No abbreviation.

<i>TetrasPool outputs</i>	<i>Abbreviations</i>	<i>Units</i>
Populations map, which displays relative populations positions	-	Meter
Intrinsic rate of increase	λ	Percent
Extinction risk	$P(ext)$	Percent
Median time to extinction	$T(ext)$	Year
Plot of the cumulative time to extinction	-	Year vs real
Plot of population and metapopulation trajectories	-	Year vs real
Histogram for 13 quasi-extinction thresholds	-	Integer vs real
Dispersal summary plot	-	Real
Extinction risk sensitivity	-	Percent

Sensitivity analysis indicates which parameters have the greatest influence on persistence time estimates (Figure 3.2). It is a fundamental part in PVA process because it allows key life-history parameters identification and management options ranking.

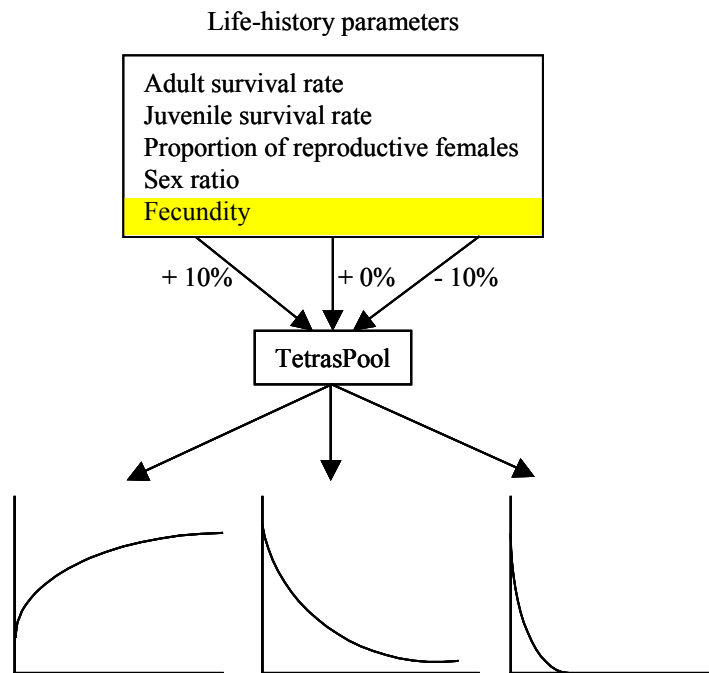


Figure 3.2. Schematic representation of the sensitivity analysis process. The default simulation is first runned without changes in parameters value (+ 0 %, central graph) and shows a clear population decline. The sensitivity analysis is then runned with a + 10 % change in one parameter value (here, I chose to examine change in fecundity value, left graph) and then with a – 10 % change for the same parameter (right graph). The PVA model is very sensitive to fecundity value because contrasted population trends were predicted.

TetrasPool allows small changes in one parameter value, all other being held constant. Simulations are then runned for all replicates over the specified time horizon. Informations on trajectories, median time to extinction and dispersal synthesis could be used to classify management options. The detailed algorithm is presented in Appendix 1. The software TetrasPool (Sachot, 2000) is available at our website (<http://www.unil.ch/tetraspool.html>).

3.4. Discussion

3.4.1. Model and stochasticity

Readily available PVA softwares propose a large array of mechanisms and process but these may be inappropriate for the species in concern or may even be confusing for the user. Our choice of specifically designed metapopulation model facilitates the incorporation of available knowledge on capercaillie. TetrasPool fits grouse biology and avoids parameterization drawbacks inherent to available softwares. The model accounts for both demographic and environmental stochasticities (including catastrophic events).

Small populations of less than 10 individuals are not adequately modeled by PVAs (Burgman et al., 1993). Such reduced population is highly influenced by stochasticities and additional effects (e.g. Allee effect, genetic factors) could also depress population growth (Nunney and Campbell, 1993; Schaffer, 1981). At low population densities, minor changes in parameters values invariably modify population destiny. As Possingham and Davies (1995) suggest, individual-based models may be more precise at very low population sizes. But in practice, land managers usually have to determine species extinction risk before small population sizes arise and I consequently designed TetrasPool. In my model, setting an extinction threshold under which the species is assumed to be extinct can solve problems encountered with low population sizes. The resulting quasi-extinction risk is a probabilistic estimation of chances to fall under the fixed threshold.

In a metapopulation structure, populations could experience dissimilar environmental variations. For example, populations located on north slopes are submitted to summer storms while south-oriented population benefited of sunny conditions. Such weather differences inequitably affect vital rates and in turn extinction risk. To examine this effect, I describe a pattern of correlated environmental variations without detailed description of underjacent mechanisms, as data are often inadequate to estimate weather conditions, or vital rates, in distinct populations. Based on capercaillie biology (Moss and Weir, 1987a; Moss and Weir, 1987b), modeled correlations affect the proportion of females with chicks. I think it is worthwhile to include environmental correlation in some simulations but user should keep in mind that these correlations are estimates and not absolute values.

Genetic aspects are not incorporated into my model, as influences of inbreeding depression or genetic variability reduction on life-history parameters are largely unknown. The genetic structure is likely to affect population persistence or life-history parameters in small, isolated populations (Bouzat et al., 1997). Small populations connected with dispersal should experience less severe influence of genetic diversity loss than small, isolated populations (e.g. Piernney et al., 1998).

Accurate datas over a long time period and good species life-history knowledges are required to make reliable quantitative prediction from PVA. When inadequate datas exists for one or more life-history parameters, they must never be drawn from datas collected for related species (Reed et al., 1998). Sparse or imprecise data on life-history parameters or partial species behaviour knowledge strongly decrease PVA predictive power and could lead to misleading conclusions (Reed et al., 1998).

TetrasPool reflects the spatial structure of populations, as behaviour and persistence of a single large population are likely to differ for several small populations (Burgman et al., 1993). Most natural populations have been subdivided into spatial subunits as a result of habitat fragmentation processes (Aberg, 1996; Boswell et al., 1998). Connectivity between subunits is achieved by dispersal events. Therefore, spatially explicit population models are powerful tools to address the complexity of population dynamics within heterogeneous landscapes (Breininger et al., 1998).

3.4.2. Dispersal

TetrasPool allows juveniles to disperse in random or directional (to other populations) directions. The « Random direction » mode is designed for blind species that have no perception of habitat types outside their initial habitat. Dispersal occurs in a random direction

until individuals encounter vacant territories in suitable habitats. When neither suitable habitats nor free territories are available in the selected random direction, individuals are assumed to be dead. This is the only mortality event linked with dispersal in TetrasPool. In my model, main adult and juvenile mortality events occur after dispersal.

The « Directional direction » mode fits species having some way to discern habitat types close to their habitat. Censusing conditions far away from their habitat is impossible (i.e. habitat types and population densities in targets populations are unknown). Individuals are assumed to explore populations around their initial habitat until they find a free territory. These behaviour and dispersal mode are highly consistent with demographic and telemetric field data recorded for several species of birds (e.g. hazel grouse (Swenson, 1991), pheasant (*Phasianus colchicus*)(Perkins et al., 1997), gulls (*Larus occidentalis*)(Spear et al., 1998)) and mammals (e.g. edgehog (*Erinaceus europaeus*)(Doncaster et al., 2001), caribou (*Rangifer tarandus caribou*)(Stuart-Smith et al., 1997), lynx (*Lynx lynx*)(Slough and Mowat, 1996)).

3.4.3. Habitat and carrying capacity

In TetrasPool, the carrying capacity does not depend on local habitat quality (i.e. inside patches, individuals are not allowed to adjust their home range from local habitat suitability). Therefore, user-defined home range values should represent the mean home range size calculated for different habitat quality within study site. Life-history parameters are not influenced by habitat quality. No dynamic evolution is associated to habitat quality so that carrying capacity remains identical throughout simulations.

A ceiling type of density dependence usually exists for territorial species that compete for breeding territory establishment (Hastings, 1996). Thus, I modelled carrying capacity at the onset of the breeding season as the upper limit of population size, itself related to the total number of available breeding territories.

3.4.4. Sensitivity

The sensitivity analysis has two important uses in conservation biology (De Kroon and Van Groenendael, 1986; Burgman et al., 1993). First, this process allows detecting crucial life-history stages and key parameters. Thus, sensitivity analysis is of great help to focus conservation effort adequately (Reed et al., 1998). For example, Gaona et al. (1998) found adult survival rate of Iberian lynx (*Lynx pardinus*) led population dynamics, suggesting that management strategy should focus on restoring habitats and reducing mortality of adults rather than promoting young cubs survival. Second, model sensitivity to small changes indicates parameters to estimate more precisely in the field (Burgman et al., 1993). For example, Bustamante (1996) simulated bearded vulture (*Gypaetus barbatus*) viability and showed that model results were largely determined by adult mortality, which was inexactly known. He suggested employing radio transmitters to monitor individual fate and determine this important life-history parameter.

Thus I conclude that PVAs simulations should always include a sensitivity analysis, which is the major and most useful result of all available simulations outputs for conservation biologists and land managers.

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4.1. Abstract

1. The populations of capercaillie, the largest European grouse, have seriously declined during the last century over most of their distribution in western and central Europe. In the Jura Mountains, the relict population is now isolated and critically endangered (less than 500 breeding adults).
2. I developed a simulation software (TetrasPool) that accounts for age and spatial structure as well as stochastic processes, to perform a viability analysis and explore management scenarios for this population capitalizing on a 24 years-long series of field data.
3. Simulations predict a marked decline and a significant extinction risk (10.4 %) over the next century, largely due to environmental and demographic stochasticity (average values of life-history parameters would otherwise allow stability).
4. Sensitivity analyses suggest focusing conservation efforts, not only on enhancing adult survival (as often advocated for long-lived species), but also on minimizing risks of brood failure and juvenile mortality (arising from different sources of disturbance). The juvenile stage matters, partly because it ensures connectivity among patches.
5. Comparisons of several management scenarios show that, in addition to the above efforts, the carrying capacities of existing patches should be improved whenever possible. The sizes of target patches, as well as their spatial localization within the study area, seem largely irrelevant issues.

4.2. Introduction

Habitat loss and fragmentation is threatening an increasing number of species. Fragmentation breaks down large natural populations into series of small-sized demes, which are highly susceptible to stochastic fluctuations and local extinctions (Akçakaya and Baur, 1996; Fahrig, 1997). This, however, does not necessarily lead to a global extinction: fragmented populations may survive for some time in disequilibrium dynamics, if the specific dispersal ability and landscape structure allows recolonization events to balance local extinction rates (Gutiérrez et al., 1999). Such metapopulation dynamics is becoming a central issue in conservation biology (e.g. Hanski et al., 1996).

Population viability analyses (PVA) are aimed at assessing the extinction risk of focal populations within a specified time horizon, and to compare alternative management options (Akçakaya and Burgman, 1995; Bustamante, 1996; Schneider and Yodzis, 1994). The introduction of quantitative elements into risk assessment is indeed crucial if management decisions are to be made on a priori clear expectations of population responses, and not on the ease of implementation or accessibility of a life stage (Crouse et al., 1987).

Analytical approaches are only of limited help in this context: the simplifying assumptions made for tractability are normally incompatible with the complexity of real situations. Details of life-histories and spatial structures in particular can usually not be dealt with analytically, but have important consequences on populations (Burgman et al., 1993; Hanski, 1991). Computer simulations, as an alternative, have the potential to account for a great deal of biological realism. But they also incur some risks and limitations, due to their lack of generality, and to the difficulty of converting real-world complex interactions into a functional model (Reed et al., 1998). Introducing too much complexity in a model is not only useless, it may be detrimental. Sophisticated models may require too detailed field information without providing much additional insights. To be useful and reliable, PVAs require careful parameter estimations (Saether et al., 1998), which are often missing or imprecise for rare or endangered species. The trade-off between complexity and functionality is thus bound to depend on the characteristics of the species in concern, on the availability of data, and on the question addressed (Burgman et al., 1993).

In the present chapter, I present a viability analysis for a highly-endangered capercaillie metapopulation from the Jura Mountains, western central Europe. Field studies of this focal metapopulation started in 1976 and have continued uninterrupted since. Its decline and specific life-history parameters are thus well documented. My analysis is based on a series of computer simulations performed with the software TetrasPool (Sachot, 2000), specifically developed to make full use of the detailed information available, but readily usable for the PVA of any species with similar life history.

4.3. Material and Methods

4.3.1. Populations

The 35 capercaillie forest patches, 24 of which in France (Montadert and Chamouton, 1997) and 11 in Switzerland (Dändliker et al., 1993), covering 542 km² in total (Figure 4.1, Appendix 2) were used for PVA.

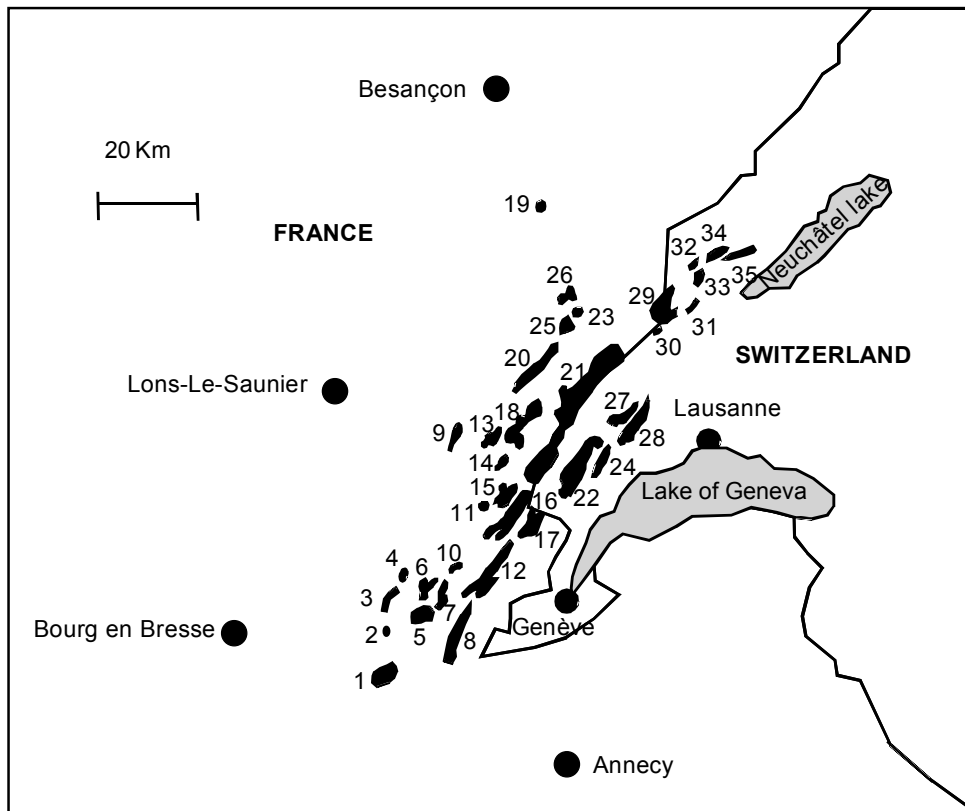


Figure 4.1. Locations of the 35 capercaillie populations in the Jura Mountains. Refer to Appendix 2 for relationships between population number, initial abundance and estimated carrying capacities.

4.3.2. Home range and breeding biology

Most of the life-history parameter values used in my simulations (means and standard deviations) stem from a long-term field study (1976-1999) of the French Jura population n° 21 (Table 4.1). Original data and details of the collecting methods were obtained from Leclercq (1987c) and Leclercq et al. (1997). When no local information was available (data on dispersal and home ranges), I used values from the literature on other west-European populations instead (Ménoni, 1991; Storch, 1993b; Wegge et al., 1981).

Capercaillie is a long-lived species, with relatively high adult annual survival rate, estimated to 0.80 ± 0.1 (SD) for females in the Jura Mountains (Leclercq, 1981). By contrast, yearling mortality is quite high, mostly during the first winter, after individuals have dispersed from their natal territory (Kastdalen and Wegge, 1990; Leclercq, 1981; Picozzi et al., 1999; Storch, 1994). Juvenile survival in the Jura population was estimated to 0.2 ± 0.1 (SD).

Females reach maturity at their first year, and then establish a breeding territory. Average clutch size was estimated to $8.0 \text{ eggs} \pm 2.0$ in the focal population. Bad climatic conditions (heavy rains) and disturbance (by humans and predators) are known to induce brood failure in capercaillie (review in: Ménoni, 1994b). A second brood is sometimes laid if the first clutch fails (Storaas and Wegge, 1984). From the information available on the focal population, only 25 % of the females succeed in rearing a brood. Males adopt a lekking strategy and play no role in acquiring or defending breeding territories, building nests or caring for young.

Table 4.1. Values calculated from long term data set (1976-1999) used for simulations; included growth rate sensitivity and elasticity for demographic parameters.

<i>Parameters</i>	<i>Symbol</i>	<i>Value ($\bar{x} \pm SD$)</i>	<i>Sensitivity</i>	<i>Elasticity</i>
Adult survival rate	p_a	0.8 ± 0.1^a	1	0.8
Juvenile survival rate	p_o	0.2 ± 0.1^a	1	0.2
Proportion of reproductive females	p_r	0.25 ± 0.2^a	0.8	0.2
Sex ratio	s_r	0.5^a	0.4	0.2
Fecundity	s_b	8 ± 2^a	0.025	0.2
Female home range size (ha)		50^b		
Home range overlap (%)		0^b		
Average dispersal distance (m)		8000^c		
Dispersal rate		0.1 ± 0.2^d		

^a From Leclercq (1987 and unpublished datas).

^b Breeding home range from Bavarian Alps and Pyrenees (Storch, 1997; Ménoni, 1991).

^c Medium value from Sweden and Finland (Wegge et al., 1981; Koivisto, 1963).

^d From Pyrenees (Ménoni, 1991).

Juveniles disperse away from the natal territory after fledging (autumn and early winter). The rate of dispersal to other patches was estimated to 10 % in a French population from the Pyrenees (Ménoni, 1991). Dispersal distances range 0.9 to 25 km for female juveniles, with some variance among populations presumably due to differences in their spatial structure. For instance, average values of about 2.7 km were documented in Sweden (Wegge et al., 1981), versus 12.8 km in Finland (Koivisto, 1963). Adults, by contrast, are extremely philopatric (Storch, 1993a; Wegge and Larsen, 1987).

Adult home range size varies greatly according to sex, season and habitat quality. Females have smaller ranges than males and select a wider range of forest structure (Storch, 1995). Birds living in optimal forests with old, widely-spaced trees and continuous bilberry layer have non-overlapping annual home ranges of size 50-100 ha (Ménoni, 1994a). Annual ranges are larger and may overlap in suboptimal conditions, reaching 550 ha in average (but up to 1000 ha) in the Bavarian Alps (Storch, 1995). But summer home ranges, in that case, are much smaller (around 150 ha). Similar values have been registered in Scandinavia and Pyrenees (Larsen et al., 1981; Rolstad et al., 1988; Ménoni, 1996).

4.3.3. Simulations

Initial population size values were always set according to actual field estimates (Appendix 2). All simulations included both demographic and environmental stochasticity and consisted of 1000 replicates run over a 100 years time horizon. A first set of simulations was based on the default parameter values provided in Table 4.1. Further simulations were then conducted after a 10 % increase or decrease of these values, in order to provide sensitivity analyses. I also conducted sensitivity analyses on a larger scale for home ranges, dispersal rate and environmental correlations, as I had little local information on these parameter values. Finally, I tested a series of management scenarios corresponding to improvements in habitat availability and / or quality. Present political context and financial resources make habitat enhancement of one third of the available area a reasonable and realistic measure. Habitat availability improvements consisted in a 30 % increase of the surface of 1) all the 11 Swiss patches, 2) the two largest Swiss patches only, 3) the seven smallest Swiss patches only, 4) the possibility to create seven new patches in the Swiss part of the metapopulation, 5) all the 24 French patches. Each of these scenarios was tested with a) the standard parameter values

provided in Table 1, as well as with a 2 % increased per capita growth rate, assumed to result from improvements in b) adult survival rate, c) female reproductive rate, or d) juvenile survival rate. This resulted in a total of $5 \cdot 4 = 20$ different management scenarios.

4.4. Results

4.4.1. Population persistence

A first point to note is that, if implemented in a deterministic life-history model, the standard values of parameters used in my simulations (Table 4.1) would result in perfect stability, since $\lambda = p_a + p_r p_o S_R b = 1$. Capercaillie populations would thus be self-replacing, and extinction risk would be null. The sensitivities of this growth rate to the life-history parameters a_i were computed as partial derivatives, $s_i = \partial\lambda/\partial a_i$, and elasticities as relative sensitivities, $e_i = s_i a_i / \lambda$ (Caswell, 1978). As shown in Table 4.1, the deterministic growth rate is highly sensitive to adult survival ($s_{p_a} = 1$), juvenile survival ($s_{p_o} = 1$), and proportion of reproductive females ($s_{p_r} = 0.8$). It is less sensitive to offspring sex ratio ($s_{S_R} = 0.4$) and least sensitive to fecundity ($s_b = 0.025$). Elasticity by contrast is large for adult survival (0.8), but smaller for all other parameters (0.2). The deterministic growth rate is obviously insensitive to dispersal rate and distance.

Contrasting with this deterministic model, computer simulations involved density dependence, stochasticity, and spatial structure. These simulations exhibited a consistent population decline (final population size 31 individuals \pm 31 (SD)), and a moderate extinction risk (10.4 %) for the next 100 years. Elasticity, calculated for a ± 10 % parameter change, is highest for adult survival, both in terms of final population size and extinction probability (Table 4.2; Figure 4.3).

Table 4.2. Model elasticities to life-history parameters changes of $\pm 10\%$.

<i>Parameters</i>	<i>Value</i>	<i>Final population size</i>		<i>Probability of extinction (%)</i>		<i>Median time to extinction (years)</i>	
		+ 10%	- 10%	+ 10%	- 10%	+ 10%	- 10%
Adult survival	0.88 ; 0.72	428 (49)	8 (14)	0	47.2	- ^a	83
Juvenile survival	0.22 ; 0.18	80 (51.6)	9 (15.4)	1.6	41.7	92	85
Proportion of reproductive females	0.275 ; 0.225	86 (55)	8 (15.6)	1.2	44.2	87.5	83
Sex ratio	0.45 ; 0.55	75 (52.2)	9 (15.3)	0.9	37.9	90	84
Fecundity	9 ; 7	92 (56.4)	7 (13.2)	0.8	51	91	82
Average dispersal distance	8800 ; 7200	30 (30.4)	33 (34.1)	11.2	10.6	88.5	88
Dispersal rate	0.11 ; 0.09	31 (30)	29 (31.7)	8.7	12.3	88	88

^a No extinction event recorded.

A 10 % increase in adult survival is enough to maintain the population stable and to eliminate any extinction risk over the time horizon considered. Elasticity is markedly lower for juvenile survival, proportion of reproductive females, fecundity, and sex ratio. A 10 % increase in one of these parameters is insufficient to completely eliminate extinction risk, and does not prevent population decline.

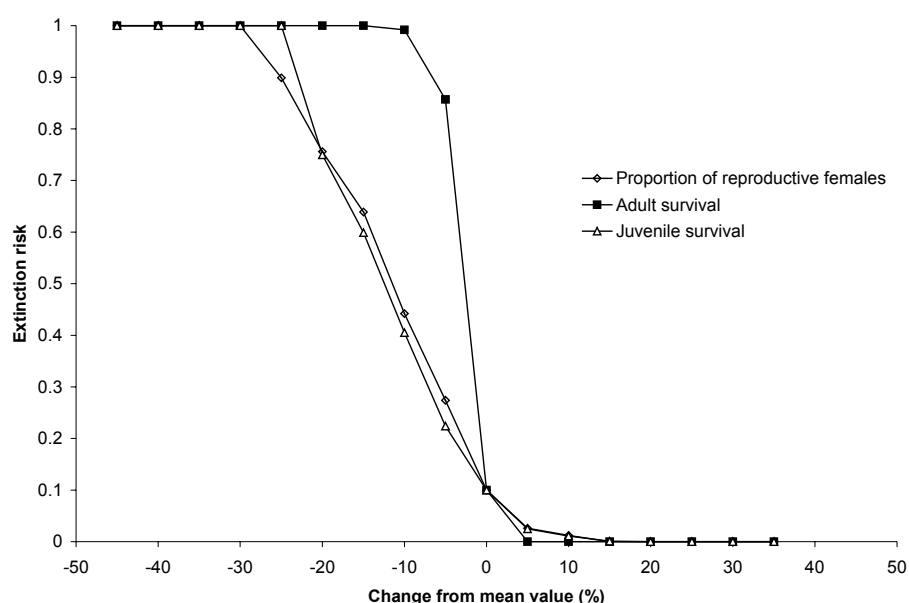


Figure 4.3. Relationships between changes in demographic parameters and extinction risk for 100-year capercaillie population simulations.

Dispersal rate and distance, finally, have very little effect: neither final population size nor extinction risk is significantly affected by a 10 % change in these parameters. Larger changes may have more marked effects: absence of dispersal would double the extinction risk, while complete dispersal would halve it (Table 4.3). In between these extremes, however, the sensitivity curve is rather flat, so that precise field estimates of these parameters are clearly not urgently required. Similarly, environmental correlations had to reach very high values (100 %) before producing any marked effect (Table 4.3), and therefore do not seem to deserve large investment in terms of field investigations. By contrast enhancing home range sizes strongly increases extinction risk (Table 4.3). This comes as no real surprise, since the carrying capacities of the different patches decrease simultaneously. Precise delineation of home range sizes and carrying capacities thus deserve closer investigations.

Table 4.3. Results of a PVA examining changes in home range size, dispersal rate and environmental correlation for the Jura capercaillie metapopulation, projected for 100 years.

<i>Scenario</i>	<i>Population size</i>		<i>Probability of extinction (%)</i>	<i>Median time to extinction (year)</i>
	<i>Mean</i>	<i>SD</i>		
No change	31	31	10.4	89
Home range increased by 100%	10	14	81	34
Home range increased by 200%	1	4	80	68
Dispersal rate decreased to 0%	23	27	19	86
Dispersal rate increased to 25%	36	32	6	92
Dispersal rate increased to 50%	39	30	5	91
Dispersal rate increased to 75%	38	28	4	92
Dispersal rate increased to 100%	47	37	4	91
Environmental correlation from 0 to 25%	39	37	9	91
Environmental correlation from 0 to 50%	36	37	10	90
Environmental correlation from 0 to 75%	31	38	17	88
Environmental correlation from 0 to 100%	28	39	22	83

4.4.2. Spatial population structure

Source and sink populations can be identified by plotting for each patch the mean number of immigrants versus the mean number of emigrants (Figure 4.4). As can be seen, the average dispersal rate is weak. Many populations export or attract less than 0.5 individuals per year, with a maximum value of 2.2 for emigration (pop. n° 21) and 1.05 for immigration (pop. n° 17). The two largest patches (numbers 21 and 22) clearly behave as source populations, while patches 24 and 27 behave more as sink populations, that persist only thanks to continuous immigration. All others patches lie near the compensation line (diagonal) with, however, an excess of slight sinks (mostly small populations; Appendix 2).

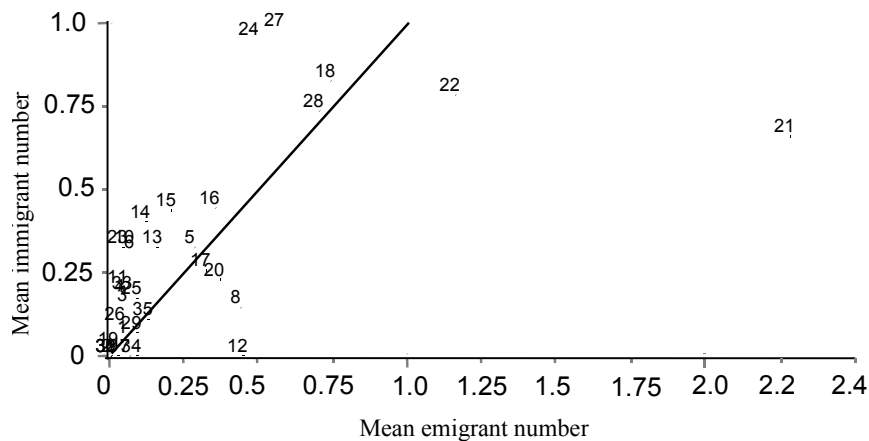


Figure 4.4. Mean emigrant vs immigrant number for 100-year capercaillie population simulations. Numbers refer to population numbers. See Appendix 2 for relationships between population number, initial abundance and estimated carrying capacities.

4.4.3. Management scenarios

From the above results, adult survival, juvenile survival and proportion of reproductive females, together with the size and possibly spatial localization of patches, were the parameters most likely to affect population viability, while being somewhat amenable to human alteration. They were thus chosen as targets for my management scenarios.

A first assessment with default parameters showed a very small impact of the different management options on extinction risk (Table 4.4). By contrast, the same scenarios with a 2 % change in per capita rate of increase showed significant improvements, in terms of both final population size and extinction risk, especially when this increase resulted from enhanced adult survival. The second best improvement resulted from enhancing the proportion of reproductive females, and juvenile survival ranked third. The five patch-management scenarios envisaged had roughly similar consequences, though the one dealing with the seven small Swiss patches only (scenario 4) appeared slightly less efficient than the one improving the 24 French patches (scenario 5). By and large, this comparison suggests that the most effective silvicultural strategy would be to improve the carrying capacities of many patches, independently of their status, and not to focus on new patches or source populations.

Table 4.4. Results of a PVA examining habitat improvement for the Jura capercaillie metapopulation, projected for 100 years.

Scenario ^a	λ	Parameter value ^b	Population size		Probability of extinction (%)	Median time to extinction (years)
			Mean	SD		
No change	1	-	31	31	10.4	89
1	1	-	36	36	9.5	88
2	1	-	33	35	9.8	87
3	1	-	29	30	11.1	88
4	1	-	34	34	9	90
5	1	-	37	36	7	91
1	1.02	$p_a=0.82$	113	65	0.3	96
2	1.02	$p_a=0.82$	101	57	0.1	85
3	1.02	$p_a=0.82$	93	54	0.6	79
4	1.02	$p_a=0.82$	103	57	0.3	90
5	1.02	$p_a=0.82$	116	64	0.2	91.5
1	1.02	$p_o=0.22$	96	64	1	93
2	1.02	$p_o=0.22$	83	56	1.2	97
3	1.02	$p_o=0.22$	78	51	1.3	91
4	1.02	$p_o=0.22$	96	58	0.1	86
5	1.02	$p_o=0.22$	95	61	0.8	96
1	1.02	$p_r=0.275$	101	65	1.2	93.5
2	1.02	$p_r=0.275$	91	60	0.8	88
3	1.02	$p_r=0.275$	90	56	0.6	88
4	1.02	$p_r=0.275$	101	59	0.6	86
5	1.02	$p_r=0.275$	107	63	0.3	95

^a K is increased by 30 % in the 11 Swiss populations (scenario 1), in the two major Swiss source populations (scenario 2), in the seven small northern Swiss populations (scenario 3), seven new patches are created in Switzerland (scenario 4), K is increased by 30 % in the 24 French populations (scenario 5).

^b -, no change in parameters values ; p_a , adult survival ; p_o , juvenile survival; p_r , proportion of reproductive females.

4.5. Discussion

Our deterministic approach and computer simulations provided quite contrasted results on two important issues. First, the deterministic model, based on the life-history parameter values sampled from the Jura population, predicted a stable situation, while my simulations showed a marked decline. This difference is mostly due to the demographic and environmental stochasticities integrated into computer simulations. On the long term, the fitness of a population depends on the geometric mean of its growth rate, which is always lower than the arithmetic mean, and the more so that the variance is large (Burgman et al., 1993).

Second, in the deterministic model, adult survival was the only parameter presenting a high elasticity, an outcome perfectly in line with the results from Leclercq (1987a). Based on

a deterministic model focusing on population n° 21 (i.e. with no spatial structure), this author also showed adult survival to have a major influence on population viability, while juvenile survival and the proportion of reproductive females had only weak effects. By contrast, my computer simulations showed elasticity for juvenile survival and female reproductive rate to be nearly as high as for adult survival.

I interpret this difference as a consequence of the spatial structure of the model. The population under study is made of several interconnected demes. Juveniles, being the only dispersing stage, are thus likely to affect its dynamics, by rescuing vanishing demes or recolonizing extinct patches. The relevance of female reproductive rate may actually receive a similar interpretation: The number of clutches produced and the survival of juveniles might become key parameters under non-equilibrium dynamics, since they provide the most effective way to counteract local patch extinction.

In long-lived birds, adult survival has often been advocated as being the main parameter on which conservation actions should be taken (Trouvilliez et al., 1988) and my results indeed confer high elasticity to this parameter. However, I argue that elasticity may actually not always be the most relevant index. Adult survival rate is four times higher than juvenile survival, so that an elasticity analysis actually compares the consequences of changes four times higher in adult survival than in juvenile survival. In practice, an increase in adult survival from 0.80 to 0.88 is certainly much more difficult to achieve than an increase in juvenile survival from 0.20 to 0.22. Indeed, it might actually be easier to enhance the values of juvenile survival and female reproductive rate, since both are presently low, than adult survival, which is already high. I think that conservation measures aimed only at improving adult survival, based essentially on an elasticity analysis, would be misleading.

Our claim is consistent with empirical observations that chick survival has large effects on population fluctuations among Galliformes (Bro et al., 2000). Similarly, the demography of a Scottish population studied by Moss et al. (2001) showed the overall decline to be due to a reduced recruitment of young birds as much as to an increased mortality of adults (in relation with forest fences collisions).

4.5.1. Spatial population structure

By and large, my simulations show only limited responses of the metapopulation dynamics to changes in the parameters linked to its spatial structure and connectivity. Dispersal rate, as well as the spatial correlations in environmental stochasticity, do, however, have significant effects when extreme values are considered (Table 4.3). Complete dispersal would halve extinction risk, while complete philopatry would double it. Similarly, a perfect correlation of female reproductive rate over the whole study area would double extinction risk. Both results are in line with my above interpretation of the importance of juvenile stages. Note, however, that the high survival rate of adults certainly helps in damping the detrimental effects of environmental stochasticity in reproductive rate.

Dispersal distance, by contrast, has very limited effects, presumably because of the close spatial proximity of the several patches forming the metapopulation. Mean distance between two adjacent patches is 4.6 ± 2.4 km, while capercaillie dispersal abilities are well beyond this limit. Telemetric studies recorded seasonal capercaillie movements up to 10 km in mountain habitats (Ménoni, 1991; Storch, 1993a). Within the present-day Jura network of patches, capercaillie dispersal abilities ensure correct connectivity for even the most remote of the

occupied patches. However, the point remains that some suitable patches may still be out of reach in regions outside my study area.

Finally, it is interesting to note that the variance in patch size seems to generate a source-sink dynamics: the only two large patches behave as sources, while small patches behave mostly as sinks. This pattern presumably arises from simple demographic processes: small patches go extinct more often through demographic stochasticity, and are thus more often in the situation of receiving immigrants, rather than producing emigrants.

4.5.2. Model limitations

A widespread shortcoming of PVAs is the lack of accurate estimations of parameter means and variances (Reed et al., 1998). In this respect, a main strength of the present analysis is that it relies on an unusual 24-years long data base, specifically collected for the population I am modelling. This situation certainly confers a great deal of confidence to my results.

Obviously, my model also has a series of limitations, the first of which concerns density dependence. I implemented a ceiling type of density dependence, which may be disputable both at high and at low densities. Territory size and / or resources may decrease progressively as density increases, which would result in a logistic, rather than ceiling-type, fitness curve. This is a minor concern, however, as high density is unlikely to create acute problems in declining populations. The behavior of the model at low density is certainly more relevant. The ceiling curve assumes a constant per capita growth rate as long as the population is below its carrying capacity, while the logistic model assumes a monotonic increase in per capita growth rate as density decreases. In terms of fecundity, the logistic model is not supported, as female capercaillie exhibit constant clutch size throughout its European distribution range, even in declining populations (Leclercq, 1984; Storaas and Wegge, 1984). Nothing is known, however, regarding possible responses in terms of juvenile and adult survival.

A negative effect of low density is actually more likely, in the first place because lek mating system tends then to collapse (Helle et al., 1994; Rolstad et al., 1998). Males perform solitary displays, and females have much harder time finding mates. This effect could not be introduced explicitly in my model, as TetrasPool does not deal with males and mating systems. In principle, Allee effects might be introduced through the use of quasi-extinction thresholds, i.e. by computing the probability that populations fall below an a priori fixed threshold population size (Burgman et al., 1993). I preferred not to try, having no idea of the exact shape and importance of possible Allee effects. These may actually arise from other parameters than the mating system. Stable populations and captive capercaillie have a 1:1 sex ratio at hatching, but studies on declining Scandinavian and Scottish populations documented a predominance of female chicks in autumn, especially in small brood and in years with low reproduction (Moss and Oswald, 1985; Wegge, 1980). It is unknown, however, whether this trend arises from a reduced survival of males chicks in poor conditions (young male physiology requires larger amounts of food, mainly invertebrates, that have lower availability in bad years), or an adaptive sex-ratio response of birds.

The second major limitation of my approach lies in the assumption of landscape stability. Capercaillie needs an open-forest structure, and one important reason for its decline in the Jura may lie in the modifications of silvicultural practices over the last century, that led to the closing of the forest in many places. If this trend continues, the extinction risk will obviously become more serious, and the values provided above may underestimate real threats.

However, the most relevant outcomes of PVAs do not lie in the absolute values of extinction risks they provide, but in the ranking of threats and management options (Akçakaya and Altwood, 1997; Lindenmayer and Lacy, 1995). In this respect, I do not expect the main limitations of my model outlined above to alter the ranking of threats and management options delineated in my simulations.

4.5.3. Conservation implications

Even under conservative and optimistic assumptions (no Allee effect and stable landscape structure), my simulations predict a strong decline and a moderate extinction risk over the next 100 years. The Jura population is thus doomed to extinction if no conservation measures are taken. From my sensitivity analyses, effective conservation would require several actions, aimed at improving a few key life-history parameters as well as habitat suitability.

Life-history parameters: Adult survival in capercaillie is very sensitive to human disturbance, mainly during winter. Birds are then arboreal, and minimize energy expenses by limiting their movements, feeding on the same tree for several days (Gjerde et al., 1985). Disturbances force birds to fly away, thereby increasing both energetic costs and predation risk (Ménoni et al., 1994). One option would be to limit access to the wintering areas, by orientating ski trackers and snowshoers towards less sensible places.

Female reproductive rate and juvenile survival are low, largely due to extrinsic factors including climate (cold and rainy weather), insect availability, human disturbance, and predation (Picozzi et al., 1999). Nests are often abandoned when people disturb incubating females. Access to breeding areas should be restricted, and the existing obligation to keep dogs in leashes in spring and early summer must become effective. Predation on nests and chicks can hardly be controlled directly, but positive indirect effects might result from forest management actions. Limiting forest fragmentation may efficiently control some predator species (Angelstam, 1986), while maintaining an open structure to the forests will favor ground vegetation, thereby providing food (herbs, bilberries, insects), shelter and hiding places.

Habitat suitability: In addition to the above actions, efforts should be made to increase the size of present-day patches, and / or create large new patches. This could be achieved through forest management actions. Preliminary investigations suggest that the suitability of several low-quality and presently unoccupied forest surfaces might be improved significantly at reasonable costs. Only the current state of the forest and the ease of implementation of measures should be taken into account, since the spatial localization of these new surfaces seem, from my simulations, largely irrelevant. Nonetheless, the largest unoccupied forest patches are localized nearby large capercaillie populations (e.g. Mont Sâla, Grand Risoux region). In this respect, these regions appear to be obvious targets for management.

The Jura capercaillie population is presently critically endangered. Actions at the two levels delineated here above should be initiated rapidly and simultaneously, if this population is to be saved.

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Predicting the occurrence of forest grouse at the local level

5

5.1. Abstract

1. Capercaillie and hazel grouse are endangered species occurring sympatrically throughout part of their distribution range in central Europe. Simultaneous persistence of these two grouse species in industrial forests is a challenging issue for conservation biologists, land-managers and foresters.
2. During winter 1998-2001, I quantified 42 variables on 156 capercaillie, hazel grouse and random plots in the Jura Mountains, Switzerland.
3. Both grouse species showed no preferred altitude between 1100-1600 m and selected exposure according to availability. Among eight available habitat types, capercaillie selected grazed forests more frequently than random while hazel grouse avoided it and largely preferred young stages.
4. Canopy, undercanopy and understory spruce, canopy fir and understory beech covers were the best predictors of capercaillie occurrence while hazel grouse occurrence was very well predicted by undercanopy and understory spruce, beech, rowan and willow covers.
5. Suitable habitats maintenance and grouse-adapted silvicultural practices are of prime importance for species persistence. Land-managers and foresters should promote a mosaic distribution of habitat types with a stratified vegetation layering. Canopy and undercanopy covers around 30 % with group-cuts of mature trees will allow a patchy rejuvenation. In these patches 50 % understory cover is optimal for hazel grouse while in the surrounding matrix understory cover preferentially lower than 20 % is required for capercaillie.

5.2. Introduction

Conservation of the endangered capercaillie is a preoccupying issue in the management of forest resources in several European countries (Storch, 2000). In Switzerland, the serious concerns raised by capercaillie rapid decline resulted in the release of financial support for silvicultural practices that would improve its habitat conditions. According to the umbrella concept (see: Simberloff, 1998), enhancement of capercaillie habitats should automatically help to save many other species. Nonetheless, Simberloff (1998) found that intensive management for an umbrella species is a contradiction in terms because the rest of the community to protect does not receive such treatment. Specific management may even conflict with management of other species (Simberloff, 1987).

The endangered hazel grouse occurs sympatrically with capercaillie throughout parts of their distribution range (Cramp, 1980). Although hazel grouse habitat requirements have been widely studied (Aberg et al., 1995; Lieser, 1995; Swenson, 1991; Desbrosses, 1997), little consideration has been paid for hazel grouse habitat selection within capercaillie habitat. The only study conducted in sympatric area in central Europe (Desbrosses, 1997) is issued from a small area in the Jura Mountains and is very unlikely to be representative. The few other studies (e.g. Marström et al., 1982; Swenson and Angelstam, 1993) are from Fennoscandia where forest structure, forest composition and silvicultural practices are highly different from central and occidental Europe. The Jura Mountains provide a good opportunity to assess habitat selection by forest-dwelling grouse because they hold good capercaillie and hazel grouse numbers (Schmid et al., 1998) and forestry practices are similar to other central European countries (Brassel and Brändi, 1999).

With the current rise of capercaillie management plans in central and occidental Europe, detailed investigations on sympatric hazel grouse habitat selection become a necessity. If hazel grouse effectively has different habitat requirements there, its persistence may be uncertain after intensive and specific forest management for capercaillie. A significant risk exists that forests managed for capercaillie may lead to hazel grouse decline or even to local extinctions. It is therefore important, and this was the first aim of this paper, to evaluate sympatric capercaillie and hazel grouse habitat requirements and build habitat models to predict grouse distribution. These models should involve key structural parameters to allow rapid assessment of grouse occurrence probability by foresters and land-managers. Finally, I propose recommendations on silvicultural practices to maintain or enhance suitable habitats for both species.

5.3. Species

The commonest habitat types of hazel grouse within Jura Mountains are old forest with patchy rejuvenation and young forest with an irregular structure (Desbrosses, 1997). Recent silvicultural practices include selective cutting and group cutting of mature trees and pre-commercial thinning with shrub removal. Abandon of intense young beech exploitation from 1960 onwards is an additional factor that contributed to hazel grouse extinction in most populations at low altitudes (< 1000 m) during the last 40 years (Blattner, 1998; Schmid et al., 1998). Remaining populations are patchily distributed between 1000-1550 m (Montadert and Chamouton, 1997). Estimation of metapopulation size is unavailable because this bird is highly secretive and notoriously difficult to census (Huboux et al., 1994; Desbrosses, 1987). Thereafter, mean local abundance of hazel grouse censused over 10 years was 2.08 ± 3.21 (SD) adults for 100 ha of optimal Jura habitats with annual variation between 0.94 - 3.21 birds

per 100 ha forest (Leclercq, 1987d). For informations on capercaillie biology, population trends and distribution, refer to Chapter 1.

5.4. Methods

5.4.1. Grouse and random plots

Field work was conducted during three winters (December-February), 1998-99, 1999-2000, 2000-2001. Winter investigations were performed 10 days after fresh snowfall to get sufficient detection. Sampling months and dropping search design were chosen to reduce capercaillie male social effects on habitat selection. In late winter (March-April), capercaillie cocks range use is strongly influenced by social spacing (Storch, 1995). At that time, cocks select ranges clustered around leks and established display territories. Their presence is determined not only by habitat composition in the surrounding of the lek, but also as a result of social interactions. By contrast, hens winter and late winter ranges are randomly spaced and truly reflect habitat selection (Storch, 1993b).

I used organism-centred and randomly located plots to analyse capercaillie and hazel grouse habitat selection (Bibby et al., 1997). During winters 1998-2000, I prospected 100 kilometric squares between 1100-1600 m and recorded habitat parameters on squares where both grouse species were present. Every square kilometre was explored radially from its centre towards the borders until one male, one female capercaillie and two hazel grouse droppings were discovered. To standardize research effort, grouse signs were searched during a maximum of one hour in each kilometric square. A total of 156 wintering trees used by capercaillie (78 males, 78 females) and 156 hazel grouse sites were sampled over 78 square kilometres (Figure 5.1). Signs were located at ± 10 m in the field (using compass, altimeter, and GPS), and marked on 1: 25 000 vectorial topographical maps (Federal Office of Topography). Two randomly selected points were marked on maps in the same kilometric squares where both species occurred. Capercaillie and hazel grouse being both forest species, areas outside forests were excluded from random plots. At these points, I checked for the absence of the species. Presence signs were never discovered in the 156 random plots.

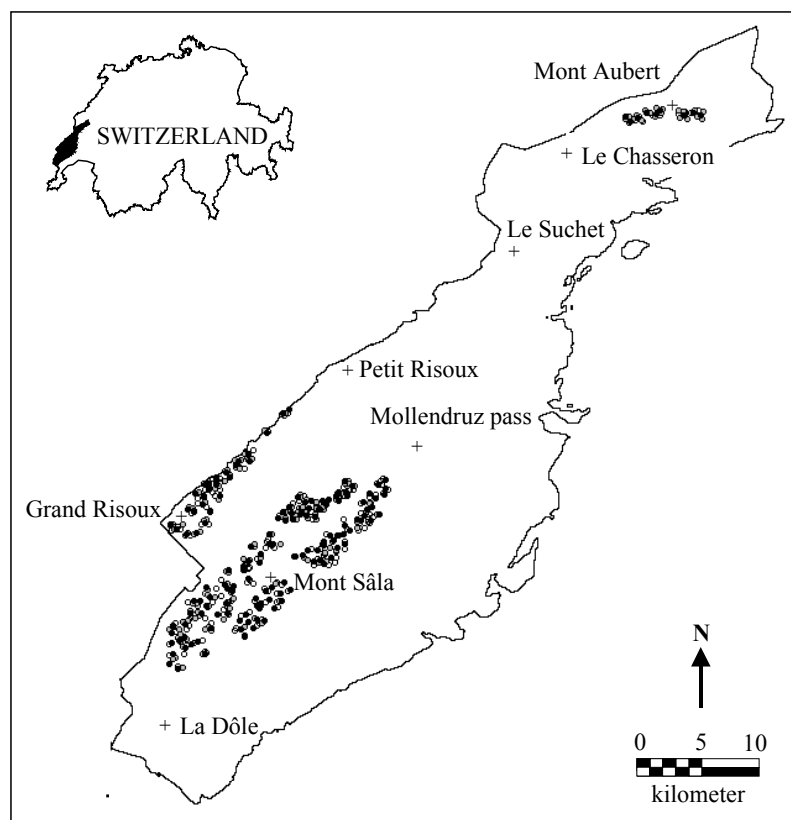


Figure 5.1. Map of the study area showing main summits and forests (cross) and plots: capercaillie presence (black circle, $n = 156$), hazel grouse presence (grey circle, $n = 156$) and random points (empty circle, $n = 156$).

5.4.2. Habitat data

For each plot, I recorded 42 habitat variables including topographical features, stand structure, composition and potential disturbance sources (Table 5.1). In the field, I used 10 m radius plots centred on each dropping or random point for variables estimation. Topographical characteristics (altitude and exposure) were measured with altimeter and compass. Elevation was directly obtained as a quantitative variable, but exposure had to be transformed using sine and cosine functions. I distinguished between eight habitat types defined by the diameter at breast height (DBH) of the dominant trees: rejuvenation (<10 cm DBH), thickets (10-20 cm DBH), pole stage (20-30 cm DBH), young forest (30-40 cm DBH), middle-aged forest (40-50 cm DBH), old forest (>50 cm DBH), wooded pasture (cattle grazed, cover < 20 %) and grazed forests (cattle grazed, cover > 20 %). Habitat structure was assessed by vegetation cover for each of the three vertical strata: (1) canopy, (2) under-canopy and (3) understory. Cover estimation was made visually following Bibby et al. (1997). An imaginary cylinder of 20 m diameter centered on the dropping or random plot and elevating through the three strata allowed eye estimation of species cover. Stand composition was characterized by measuring specific cover of 26 variables. Cover estimations were made to the nearest 5 %. Species with cover between 1-3 % were assigned a value of 1 %.

Table 5.1. Topographical, vegetation and potential human disturbance sources ($n = 42$) used to characterize capercaillie and hazel grouse wintering plots and random sites. Topographical and vegetation data are means or frequencies for a standard 10 m radius plot. For human disturbance, distances are to the nearest focal object and frequencies are for a 100 ha plot.

Abbreviation	Variable description
Topography	
ALTI	altitude [m]
SINEXPO	exposure sine [°]
COSEXPO	exposure cosine [°]
Habitat type	
HABTYPE	Categorical variable, 0 : rejuvenation (< 10 cm DBH ^a), 1 : thickets (10-20 cm DBH), 2 : pole stage (20-30 cm DBH), 3 : young forest (30-40 cm DBH), 4 : middle-aged forest (40-50 cm DBH), 5 : old forest (> 50 cm DBH), 6 : wooded pasture (cattle grazed, cover < 20%), 7 : grazed forest (cattle grazed, cover > 20%).
Canopy cover	
CANOPYC	% total canopy cover in the circular sampling area
SPRUCEC	% canopy spruce (<i>Picea excelsa</i>)
FIRC	% canopy fir (<i>Abies alba</i>)
BEECHC	% canopy beech (<i>Fagus sylvatica</i>)
MAPLEC	% canopy maple (<i>Acer pseudoplatanus</i>)
Under canopy cover	
UNDERCC	% total undercanopy cover
SPRUCEUC	% undercanopy spruce
FIRUC	% undercanopy fir
BEECHUC	% undercanopy beech
MAPLEUC	% undercanopy maple
ROWANUC	% undercanopy rowan (<i>Sorbus aucuparia</i>)
WHITEUC	% undercanopy whitebeam (<i>Sorbus aria</i>)
Understory cover	
UNDERSC	% total understory cover
SPRUCEU	% understory spruce
FIRU	% understory fir
BEECHU	% understory beech
MAPLEU	% understory maple
ROWANU	% understory rowan
WHITESU	% understory whitebeam
WILLOWU	% understory willow (<i>Salix</i> sp.)
FLYHONU	% understory fly honeysuckle (<i>Lonicera</i> sp.)
ROSEU	% understory alpine rose (<i>Rosa pendulina</i>)
LABURU	% understory laburnum (<i>Laburnum alpinum</i>)
ELDERU	% understory elder (<i>Sambucus</i> sp.)
MOASHU	% understory dwarf-medlar whitebeam (<i>Sorbus chamaemespilus</i>)
HAZELU	% understory hazel (<i>Corylus avellana</i>)
Human disturbance	
DROAD1	Distance (m) to 1, 2, 3 class roads (large roads)
DROAD2	Distance (m) to 4, 5 class roads (small roads)
DROAD3	Distance (m) to 6 class roads (trails)
DALPIT	Distance (m) to alpine ski trails
DNORDIT	Distance (m) to nordic ski trails
DSNOWST	Distance (m) to snowshoe trails
DSLEDDT	Distance (m) to sled dog trails
DHIKERT	Distance (m) to hiker trails
DFARM	Distance (m) to winter farm access
DSKILIFT	Distance (m) to skilifts
FBUILD	% buildings in a 1km ² circular area around sampling plot
FFARM	% farms
FROADS	% roads

^a DBH, diameter at breast height.

As several studies suggested disturbing effects of human activities on capercaillie (Leclercq, 1985; Ménoni and Bougerol, 1993) I included 13 variables related to human disturbance based on geographic information system (GIS) databases. Frequency of buildings, farms and roads were derived from boolean land-use data for each hectare of the Jura Mountains, obtained from the Swiss Federal Office of Statistics (Geostat database). They were transformed into quantitative ones by calculating the proportion of hectares of a given category within a 1km² circle (a surface corresponding to capercaillie habitat range) centred on the grouse and random plot locations. Distance data express the distance between grouse or random plot locations and the closest cell from a given disturbance category. Distances to the road network were calculated from data of the Federal Office of Topography (Vector25 database). Distance to nordic ski trail, alpine ski trail, skilifts, snowshoes trails and sled dogs trails were calculated from digitalized maps of leisure activities edited by the Association vaudoise du tourisme pédestre and the tourist offices from the Vallée de Joux, St-Cergue and Les Rasses. Data rasterization and extraction were performed using Idrisi32 (Clarks Lab.).

5.4.3. Data analysis

Vegetation data and data derived from GIS databases were used to analyze habitat selection (Table 5.2). Distance variables were square root-transformed and percentages were arcsine-transformed as appropriate. Significant differences in habitat composition for capercaillie cocks and hens were investigated with *t*-tests. I used Bonferroni adjustments of significance level to reduce the chance of type I error.

To quantify habitat selection by forest grouse I used both univariate tests and stepwise regression. Habitat use in relation to topography and habitat type was analyzed with χ^2 tests. Exposures dispersion was examined with Rayleigh's tests (Zar, 1984) and exposures frequencies (8 categories: N, NE, E,...) by χ^2 tests. Mean values for grouse plots and random plots were compared through *t*-tests with Bonferroni adjustments. All statistical analyses were performed on S-Plus 2000.

Univariate comparisons do not account for the multivariate structure of data. I thus used logistic regression within generalized linear model (GLM) framework to identify minimal subsets of uncorrelated factors that best explain grouse presence-absence. Before, I controlled for multicollinearity by using a Pearson correlation matrix (Sokal and Rohlf, 1995). When pairwise correlations occurred ($r > 0.5$), I dropped the variable with less biological meaning. Initial dataset was partitioned into a calibration dataset with 2/3 of presence and random data, while the remaining 1/3 was assigned to a validation dataset.

For GLM analysis I used untransformed variables, as factor normality is not a prerequisite and error terms may have non-Gaussian distributions (Guisan and Zimmermann, 2000). GLMs involve a linear predictor, an error function and a link function. Following Hosmer and Lemeshow (1989), I used a linear predictor that was a first order polynomial, a binomial error distribution and logit link function. A stepwise forward and backward selection procedure was used to select explanatory variables. Final models retained only uncorrelated variables significant at 5 % level.

Table 5.2. Comparison between 39 habitat parameters (untransformed) recorded in 156 plots for capercaillie, hazel grouse and random points in the Swiss Jura Mts 1998-2001. Differences between means for grouse and random plots (untransformed) were examined by *t*-tests, with Bonferroni adjustments: **P* < 0.05, ***P* < 0.01, ****P* < 0.001.

	Random plots		Capercaillie			Hazel grouse		
Variable	Mean	SD	Mean	SD	P-value	Mean	SD	P-value
<i>Canopy cover</i>								
CANOPYC	23.44	20.13	14.03	11.1	<0.001***	11.92	11.81	<0.001***
SPRUCEC	21.38	18.6	11.12	9.72	<0.001***	10.92	11.96	<0.001***
FIRC	0.7	3.54	1.97	2.89	<0.001***	0.57	1.95	0.009**
BEECHC	1.25	8.13	0.61	2.55	0.787	0.22	1.29	0.317
MAPLEC	0.11	0.6	0.33	1.89	0.231	0.17	0.78	0.426
<i>Under canopy cover</i>								
UNDERCC	16.85	16.24	13.28	10.21	0.058	19.28	18.23	0.543
SPRUCEUC	11.66	13.09	7.66	7.37	0.003**	15.10	16.71	0.227
FIRUC	0.64	6.43	2.37	2.82	<0.001***	1.30	3.08	<0.001***
BEECHUC	2.83	6.26	2.07	5.04	0.349	1.92	5.99	0.168
MAPLEUC	1.44	3.32	1.22	2.73	0.618	0.99	2.78	0.019
ROWANUC	0.04	0.29	0.03	0.24	0.680	0.15	0.70	0.150
WHITEUC	0.21	2.02	0.00	0.00	0.094	0.00	0.00	0.044*
<i>Understory cover</i>								
UNDERSC	28.13	28.63	17.53	19.81	<0.001***	47.65	25.34	<0.001***
SPRUCEU	6.01	12.85	4.96	6.92	0.631	17.89	18.88	<0.001***
FIRU	1.08	4.54	1.00	1.95	0.057	2.18	8.27	0.011*
BEECHU	11.76	23.48	5.45	12.42	0.020*	11.44	21.96	0.523
MAPLEU	2.62	7.32	2.49	4.91	0.773	4.55	8.51	0.001
ROWANU	4.29	8.93	2.99	6.71	0.129	10.26	13.08	<0.001***
WHITESU	0.4	1.2	0.32	0.80	0.163	0.44	0.28	0.547
WILLOWU	0.15	0.44	0.07	0.28	0.083	1.27	4.18	<0.001***
FLYHONU	0.47	2.49	0.25	0.95	0.279	0.24	1.26	0.168
ROSEU	0.02	0.18	0.01	0.08	0.478	0.04	0.41	0.654
LABURU	1.25	6.39	0.31	3.76	0.046	0.65	5.17	0.412
ELDERU	0.02	0.14	0.01	0.08	0.315	0.20	2.40	0.660
MOASHU	0.06	0.36	0.00	0.00	0.019*	0.01	0.11	0.151
HAZELU	0.00	0.00	0.00	0.00	- ^a	0.01	0.08	0.320
Human disturbance								
DROAD1	428.99	356.24	440.46	315.2	0.475	404.62	306.89	0.893
DROAD2	111.96	89.28	133.19	104.95	0.177	106.85	89.84	0.388
DROAD3	476.63	341.95	509.53	339.75	0.393	470.91	443.50	0.163
DALPIT	3842.19	1780.14	3761.26	1771.11	0.672	3677.71	1782.09	0.622
DNORDIT	990.65	804.07	989.23	771.44	0.944	847.95	735.72	0.551
DSNOWST	34877.39	9536.3	34166.76	9397.05	0.619	33907.02	9438.86	0.154
DSLEDDT	13880.2	5964.81	14553.58	6136.77	0.38634	14904.35	6122.23	0.104
DHIKERT	14108.97	12546.6	14778.11	12389.68	0.50139	15023.88	12134.03	0.146
DFARM	4892.28	3328.61	5126.14	3361.6	0.54638	4984.32	3588.20	0.344
DSKILIFT	4827.39	1965.23	4646.42	1978.97	0.4446	4731.48	1957.12	0.231
FBUILD	0.04	0.19	0.03	0.18	0.75979	0.02	0.14	0.312
FFARM	0.01	0.11	0	0	0.15797	0.01	0.08	0.564
FROADS	0.22	0.51	0.27	0.58	0.51289	0.25	0.54	0.626

^a-, unavailable value.

Habitat models without estimation of predictive efficiency have poor validity (Monserud and Leemans, 1992). Capercaillie and hazel grouse models predictive success were assessed and compared in two ways. First, prediction accuracy was assessed by the percentage of validation data correctly assigned by models, which is among the most robust measures of prediction success (Hosmer and Lemeshow, 1989). Second, Kappa statistics was used

(Monserud and Leemans, 1992) where the κ is the proportion of specific agreement between model predictions and the validation dataset (Monserud and Leemans, 1992). When $\kappa = 1$ a perfect agreement exists but when $\kappa = 0$, agreement is no better than expected by chance (for further details, see: Monserud and Leemans (1992)).

5.5. Results

5.5.1. Grouse wintering site selection

I pooled data of males and females capercaillie for subsequent analyses, as topographical features, habitat types and habitat parameters did not differ between sexes (*t*-tests with Bonferonni correction, $P_s > 0.05$).

Both grouse species selected altitudinal ranges according to availability and showed no preferred altitudes between 1100-1600 m (χ^2 tests, $P_s > 0.05$; Figure 5. 2a). Wintering sites exposures for capercaillie and hazel grouse differed significantly from circular uniformity (capercaillie : Rayleigh's test : $R = 37.41$, $Z = 8.97$, $P < 0.001$; hazel grouse : $R = 39.00$, $Z = 9.75$, $P < 0.001$; Figure 5. 2b) as did also random plots exposures ($R = 53.15$, $Z = 18.11$, $P < 0.001$). All sets had two prevalent directions around N-W and S-E (Figure 5. 2b), which correspond to mean Jura exposures and selected exposure did not differed from random plots (capercaillie : $\chi^2 = 8.258$, $df = 7$, $P = 0.310$; hazel grouse : $\chi^2 = 8.466$, $df = 7$, $P = 0.293$; Fig. 3).

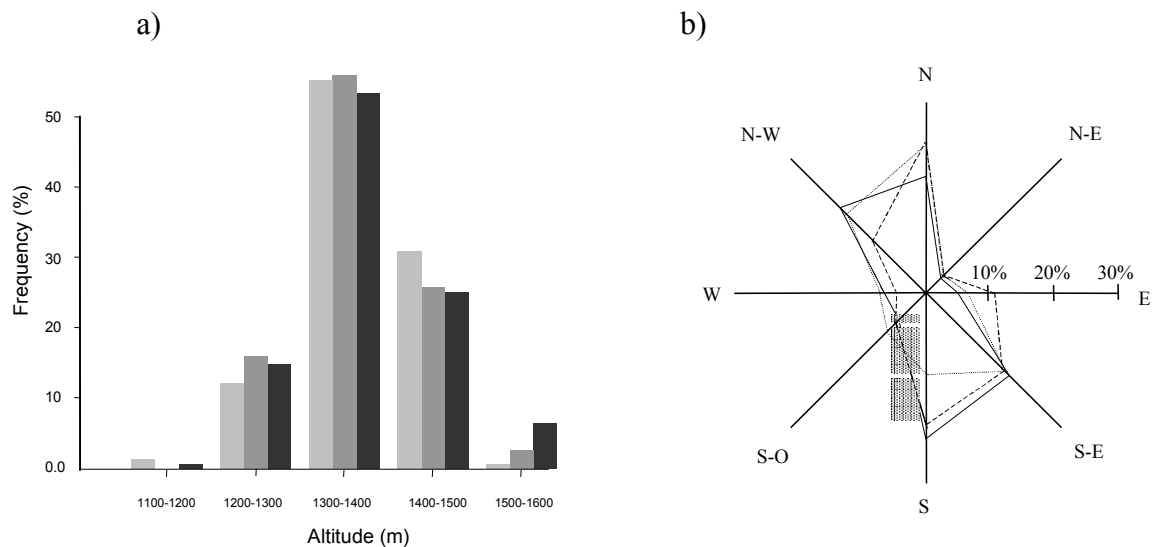


Figure 5.2. a) Distribution of capercaillie (grey), hazel grouse (dark grey) and random (black) plots in relation to altitude, b) Distribution of capercaillie (solid line), hazel grouse (dotted line) and random (dashed line) plots in relation to exposure.

Young stages (rejuvenation, thickets, pole stage, young forest) and habitat types with cattle (wooded pasture, grazed forests) seldom occurred in sampling plots ($< 5\%$ in all cases). To meet χ^2 test assumptions (Sokal and Rohlf, 1995), stages with DBH < 40 cm were grouped into a young-successional-stages category, and wooded pasture and grazed-pasture into a grazed-forests category (Figure 5.4). Overall, hazel grouse used habitat types non-randomly

($\chi^2 = 14.77$, $df = 3$, $P < 0.05$). This was merely due to strong preference for young stages ($\chi^2 = 9.02$, $df = 1$, $P < 0.05$) and grazed forests avoidance ($\chi^2 = 4.93$, $df = 1$, $P < 0.05$). By contrast, capercaillie used grazed forests more than expected ($\chi^2 = 5.77$, $df = 1$, $P > 0.05$; Figure 5.4).

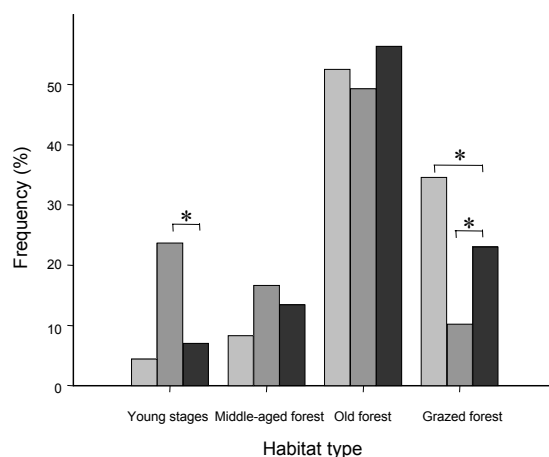


Figure 5.4. Habitat distribution of capercaillie (grey), hazel grouse (dark grey) and random (black) plots. Differences of frequencies between grouse and random plots were examined by χ^2 tests : * $P < 0.05$.

The univariate tests revealed that grouse wintering sites differed significantly from random sites regarding habitat features (Table 5.2). During winter, capercaillie tended to avoid canopy (CANOPYC) and spruce (SPRUCEC) cover and to prefer higher canopy fir (FIRC) and under-canopy fir (FIRUC) cover relative to random points. Total understory (UNDERSC) cover was lower in sites with capercaillie (Table 5.2). Surprisingly, wintering sites were not farther from human activity, and had no lower proportion of human disturbance sources in their vicinity, than random sites (Table 5.2).

Hazel grouse preferred sites with lower CANOPYC and SPRUCEC cover as well as higher FIRUC cover than random points. Additionally, hazel grouse selected sites with higher UNDERSC, understory spruce (SPRUCEU), rowan (ROWANU) and willow (WILLOWU) cover than random points (Table 5.2). Distance or frequency of human disturbances were not significantly different between hazel grouse and random sites.

5.5.2. Habitat selection modelling

I built separate GLMs for wintering site selection of capercaillie and hazel grouse. Of the 42 habitat variables, some were more or less correlated. Correlated variables, i.e. pairwise comparisons with $r > 0.5$, were removed before model construction. Therefore, ALTI, SINEXPO, COSEXPO, HABTYPE and CANOPYC, under-canopy (UNDERCC) and UNDERSC covers were excluded, while, among understory species, alpine rose (ROSEU) and elder (ELDERU) were removed. Among human disturbance sources, distance to skilifts (DSKILIFT) was excluded because of high correlation with alpine ski trails (DALPIT). Of the initial variable set, 33 variables were then used to fit the models.

For capercaillie, I obtained a model with only five variables over the three vertical strata (Table 5.3). Capercaillie occurrence probability was positively influenced with FIRC but

negatively related to SPRUCEC, undercanopy spruce (SPRUCEUC), SPRUCEU and understory beech (BEECHU). This model was significant overall. Classification accuracy was 70.2 % for all sites while 82.7 % of the presence and 57.7 % of the random points were correctly assigned. The evaluation by Kappa statistic shows a reasonable fit to the data ($\kappa = 0.461$).

Table 5.3. GLM model for winter capercaillie habitat selection with binomial error distribution and logit link function. The five retained variables explained 70.2 % of differences in habitat selection. See Table 5.1 for variable codes.

Variable	Estimate	SE	<i>t</i> -ratio	<i>P</i> -value
Intercept	1.882	0.373	5.044	<0.001
SPRUCEC	-0.071	0.013	-5.315	<0.001
FIRC	0.139	0.055	2.518	0.012
SPRUCEUC	-0.053	0.016	-3.195	<0.001
SPRUCEU	-0.035	0.149	-2.390	0.017
BEECHU	-0.026	0.009	-2.963	0.003

The hazel grouse model selected five variables over two vertical strata (Table 5.4). Occurrence probability was positively influenced with SPRUCEUC, SPRUCEU, BEECHU, ROWANU and WILLOWU covers. This highly significant model correctly assigned 77.9 % of the sites, correctly classify 69.2 % of presence and 86.5 % of random sites. Model had a good fit to the data with a Kappa statistic of 0.615.

Table 5.4. GLM model for winter hazel grouse habitat selection with binomial error distribution and logit link function. The five retained variables explained 77.9 % of differences between wintering sites and random plots. See Table 5.1 for variable codes.

Variable	Estimate	SE	<i>t</i> -ratio	<i>P</i> -value
Intercept	-2.843	0.415	-6.855	<0.001
SPRUCEUC	0.086	0.021	4.125	<0.001
SPRUCEU	0.075	0.019	3.985	<0.001
BEECHU	0.040	0.010	3.770	<0.001
ROWANU	0.102	0.025	4.005	<0.001
WILLOWU	1.072	0.435	2.462	0.014

5.6. Discussion

5.6.1. Models strengths and weaknesses

Analysis with GLMs is performant but also has some limitations (Guisan and Zimmermann, 2000). For capercaillie, only five variables were needed to correctly classify 70.2 % of sites, while five variables correctly assigned 77.9 % of sites used or avoided by hazel grouse. Lack of perfect predictive power in my models is certainly caused by a number of others influences that may contribute to grouse distribution. Proportion of edges, distance to dense cover and grouse population densities can all be expected to play a role in habitat selection but were unavailable in my study area. In the boreal forest, most hazel grouse kill-sites were located at edges between dense and normal forest or far from dense cover (Swenson, 1991). Lindén and

Wikman (1983) showed that when hazel grouse were abundant, they were distributed more evenly among the available habitats than during populations low, when the birds were concentrated in preferred habitats, and distribution became patchy. Study site delimitation and sampling design may also contribute to good but not excellent model performances. I had deliberately chosen sampling units where both grouse species occurred, in order to detect whether subtle differences in habitat occur between used and unused sites at that small observation level.

Decision on which variables should enter the model is a key phase during modelling procedures (Guisan and Zimmermann, 2000). I removed multicollinear variables as introduction of highly correlated predictors artificially inflates the degrees of freedom of inference tests. This might produce retention of useless, dependant predictors in the final model. Model interpretation could also be biased because the order of variables introduction during GLM modelling procedure matters (Guisan and Zimmermann, 2000). To reduce this drawback, predictors were selected automatically by stepwise forward and backward procedures.

Model accuracy and predictive power are enhanced when predictor variables are reduced to a reasonable number (Harell et al., 1996). Harrell et al. (1996) suggest that no more than $m/10$ predictors should be included in the final model, where m is the total number of observations. Thus my final models should retain a maximum of 15.6 variables (156/10). This condition was largely respected because final models included only five variables for every grouse species.

Despite the above limitations, models accurately predict capercaillie and hazel grouse occurrence from a subset of few, essential, environmental variables. Models simplicity combined with the ease of variable measurement provide land-managers and foresters a first tool to estimate capercaillie and hazel grouse occurrence probabilities in sympatric areas of central and occidental Europe.

5.6.2. Grouse habitat selection

Topographical features played a minor role in winter habitat selection of capercaillie and hazel grouse. Birds chose altitude and exposure according to availability and these parameters did not reflect any species preference. These results were consistent with those of Leclercq (1987a) and Desbrosses (1997) who found no relationships between grouse presence and topography in the French Jura Mts. In the Bavarian Alps, capercaillie preference for east exposures has been recorded but was related to bilberry availability, its favorite food item during the snow-free period (Storch, 1993a).

Differences in habitat type selection were evident among the two grouse species. Capercaillie selected grazed forest more than expected but hazel grouse avoided it and favored young successional stages. Grazed forests are partially grazed by cows between June-September with subsequent strong modifications of habitat structure. Their opened structure is dominated by spruce interspersed with a few fir and has a very low understory cover. These characteristics fit to capercaillie but not to hazel grouse habitat requirements, which selects moderately dense, young forest stages.

Capercaillie and hazel grouse had different needs in terms of habitat structure and composition. Capercaillie showed a strong preference for higher fir cover but lower canopy,

under-canopy and understory cover of spruce and beech, the dominant tree species. On the opposite, hazel grouse selected wintering sites with lower canopy cover, higher under-canopy fir and spruce cover as well as dense understory cover of spruce, beech, rowan and willow.

Capercaillie is the largest European grouse (Cramp, 1980) and preference for opened forest structures during winter suggests that access to wintering tree may be an important criterion for choice. Wintering tree choice is not only related to access. During winter, capercaillie feeds essentially on coniferous needles, mainly firs with high amount of nitrogen contents (Leclercq, 1987c). This superabundant, continuous supply of resources allows a reduced activity (Gjerde and Wegge, 1987) and birds to forage simultaneously in the same high quality tree (Leclercq, 1987c). Capercaillie also has a strong preference for fir located within the surrounding canopy and avoids isolated fir. In the canopy, capercaillie should gain protection from prevailing wind, (which reduce energy loss) and decrease predation risk from avian predators (Gjerde, 1991; Storch, 1993c).

Owing to smaller size, hazel grouse has different energy requirements and needs more nutritious food (Andreev, 1988). In central Europe, winter hazel grouse diet is dominated by young buds and catkins of rowan, willow and beech, the most nutritious food items available in mountain habitats (Jacob, 1988a). This may be one important reason why these tree species positively influence hazel grouse presence in my model. Winter food availability might not only determine hazel grouse distribution but also bird abundance. Swenson (1993) found strong evidence that suitable territory availability was dependent upon the abundance and distribution of alder (*Alnus* sp.), the favorite food item in the boreal forests, which was in turn limiting numbers of hazel grouse territories during winter.

Hazel grouse has numerous predators and most kills occurred during foraging activity through avian predators (Swenson, 1991). Foraging in the understory may thus reflect a compromise between optimal resources exploitation and avian predator avoidance. In the boreal zone, hazel grouse was shown to exploit food resources close to dense spruce cover (Marcström et al., 1982; Swenson, 1991). Model results are in accordance with Scandinavian studies as spruce cover also positively influenced hazel grouse habitat within Jura Mountains. There, deciduous trees (rowan, willow and beech) have low coverage during winter and are unlikely to provide sufficient cover from predators. Hence, dense understory cover of spruce in the immediate vicinity of food resources is likely to be important as cover from predators.

Capercaillie is repeatedly assumed to be highly sensitive to human disturbance (Leclercq, 1985; Ménoni et al., 1994; Brenot et al., 1996) but this bird probably responds to landscape variables at different spatial levels (Aberg et al., 2000). Within a landscape, capercaillie might first select relatively undisturbed forest patches and then specific microhabitats characteristics within patches. My results suggest that capercaillie might tolerate some human disturbance within suitable patches. Wintering sites were not farther from human activities, and had no fewer proportion of human infrastructures around, than random sites. I interpret this by the long period (from December to May) of snow-covered roads and trails that limit human interspersions into forested habitats. During winter, farms and forest refuges are unoccupied and thus do not decrease habitat suitability. Nordic ski trails are essentially traced in open pastures and rarely in forested areas and might not be prejudicial for capercaillie as long as skiers stay on the tracks network. Alpine ski structures are very local, occupying the highest summits. Capercaillie signs were never found in their vicinity and thus my results did not reflect any species avoidance or preference toward it.

Several studies reported hazel grouse indifference towards human disturbance all year round (e.g. Bernard-Laurent and Magnani, 1994; Desbrosses, 1997). I also found no tendency for hazel grouse to avoid or prefer sites with human disturbances, probably because the bird is less shy than capercaillie and very confident on its camouflage (Leclercq, 1985; Desbrosses, 1997).

5.6.3. Conservation implications

Large, endangered birds with complex mating systems (e.g. great bustard (*Otis tarda*), capercaillie) are very unlikely to return in areas where populations have been extinct (Lane et al., 2001). For these species, suitable habitat maintenance in areas where birds occur is essential for species persistence (Lane et al., 2001; Ménoni, 1994a; Storch, 2000). My results emphasize that habitat requirements of capercaillie and hazel grouse are highly different, also in their sympatric zone of occurrence. Both grouse species did not show preferences for or avoidance of specific topographical features and human disturbance sources in plots of cooccurrence. Therefore, their persistence within industrially logged forests is tightly linked to silvicultural practices. The following recommendations should be effective between 1100-1550 m, in the sympatric zone of occurrence.

Management objectives for capercaillie should account for a mosaic distribution of habitat types with a stratified vegetation layer, which implies a high structural diversity. Vertical structure should maintain total canopy and undercanopy covers around 30 % ($\bar{x} = 27.31 \pm 12.77$; Table 5.2) and an understory cover around 20 % ($\bar{x} = 17.53 \pm 19.81$). Hazel grouse necessitates similar canopy covers but an understory cover of 50 % ($\bar{x} = 47.65 \pm 25.34$). These two distinct requirements are not incompatible with sustainable forest exploitation. A patchy distribution of rejuvenation stages within old successional stages should allow both grouse species persistence. Land manager should promote horizontal forest heterogeneity over large areas, i.e. greater than 300 ha for a capercaillie population with a lek (Wegge and Rolstad, 1986), so that capercaillie establishes territories in habitats with low rejuvenation while the lesser range demanding hazel grouse selects thicker and younger habitat types.

To achieve grouse-adapted silviculture, mature trees would be preferentially group-cut, as selective cutting lead to strong, generalized rejuvenation by beech. Such habitat uniformisation could be temporarily suitable for hazel grouse but is immediately detrimental for capercaillie. On the opposite, a gap-phase rejuvenation allows species coexistence over several decades. Local creation of gap rejuvenation networks increases habitat suitability for capercaillie during the first 20 years, then rejuvenation grows and provide suitable habitats for hazel grouse while capercaillie favor older stages in the surrounding matrix.

Forest composition is also crucial. Fir is the main food during winter for capercaillie and must be maintained in high proportion. For hazel grouse, rowan and willow should be conserved and not systematically removed to promote young maple or beech. Finally, the maintenance of small groups of spruce should ensure grouse safety (from predators) and thus increase survival rate.

Some land-managers and foresters have recently applied several of the above measures on five experimental plots. Preliminary results indicate positive effects in terms of frequentation by grouse (S. Sachot, B. Leclercq, M. Montadert, unpublished data). An increase in grouse numbers was also expected (see : Leclercq, 1981; Rolstad and Wegge, 1989) but has not been observed. Obviously, habitat quality is of major importance for grouse populations setting and

maintenance but it does not necessarily implicate elevated capercaillie numbers. As Hanski (1991) suggests, local abundance also depends on the spatial structure of populations and demographic performances. Future researches should involve an extended network of experimental plots in various habitat types in order to estimate long-term efficiency and costs. Comparisons of understory removal, gap-regeneration efficiency with uncut plots and subsequent grouse frequentation are also needed. Finally, exploration of population demography with population viability analysis should enhance our understanding of additional factors influencing grouse abundance in fragmented habitats.

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Predicting the occurrence of capercaillie at the landscape level

6

6.1. Abstract

1. Capercaillie is an endangered species in the mountainous forests of central Europe. In Switzerland, financial support is available to promote silvicultural practices enhancing capercaillie habitats. Political pressures to invest money in a cost effective way inevitably called for habitat suitability maps and core areas identification.
2. In this chapter, I provide a habitat-suitability analysis for the Jura Mountains (western Switzerland), based on presence data collected from 1995 to 2000. Presence data were randomly split into equal calibration-validation datasets.
3. Habitat was described on the basis of land-use databases (one-hectare cells) including topography and vegetation, as well as human infrastructures (buildings, road and railway networks). A second set of habitat suitability maps were built from topography, human disturbance and punctual vegetation data of species cover registered on a 1 plot per 16 ha basis for the south-western part of the study area.
4. From my results, capercaillie prefers high-elevation sites and open forests with moderate canopy cover and strong bilberry cover. By contrast, meadows, thickets, buildings, farms, roads, dense canopy closure and strong beech cover largely are avoided.
5. Slope, exposure and distance to nordic ski trails do not significantly damper habitat suitability. The gentle topography of the Jura Mountains and nordic ski trails locations avoiding capercaillie breeding and wintering habitats explain the observed pattern.
6. Capercaillie occurrence at the landscape level is very adequately predicted. Model fiability is strong, predicted suitabilities are high by comparison to the validation dataset. Predicted suitability maps accuracy is also confirmed by highly significant bootstrap resampling.
7. My models allow the identification of two forest patches, the Mont Risoux and the Mont Sâla that should be targeted for management actions, because their overall suitability would be significantly improved through low-cost interventions (forest opening through selective tree cutting, and limitation of human incursions).
8. This approach allows accurate predictions of capercaillie occurrence at the landscape level. In connection with sensitivity analyses of habitat suitability, ecological-niche factor analyses have the potential to provide a valuable generalized tool for land managers and conservation biologists

6.2. Introduction

In Switzerland, the serious concerns raised by capercaillie rapid decline resulted in the release of financial support for silvicultural practices that would improve its habitat conditions. Political pressures to invest money in a cost effective way inevitably called for a comprehensive approach aimed at weighting alternative management options. High ranking among identified priorities, was the establishment of habitat-suitability and potential-distribution maps (Smith et al., 1998). Indeed, habitat improvements do not need to be performed in the immediate vicinity of already established populations. Large-scale habitat scanning might reveal potentially suitable, but presently empty patches, that could be restored at lower costs. The present study is part of a project aimed at improving habitat quality through forest management for the Swiss Jura capercaillie populations. My specific goals were 1) to update information on its present-day distribution 2) to define crucial habitat parameters at both local and landscape level, and 3) to establish a large-scale habitat suitability map that could help in weighting forest-management decisions.

6.3. Material and methods

6.3.1. Statistical methods

Habitat analyses through Geographic Information Systems (GIS) usually rely on multivariate statistics (such as logistic regressions or GLMs) that require both presence and absence data (Guisan and Zimmermann, 2000). While presence data may be definitely established by direct observation (of individuals, tracks, droppings, feathers), absence data are notoriously difficult to establish reliably (Leclercq, 1981). Presumed absences may simply result from the failure to detect presence (Weckerly and Ricca, 2000). Even large birds like capercaillie may reveal extremely cryptic (Cramp, 1980; Leclercq, 1987a). Furthermore, the species may be absent from some localities for historical reasons, which have nothing to do with habitat suitability (Catusse et al., 1992; Ménoni, 1994). The Ecological Niche Factor Analysis, or ENFA (Hirzel et al., in press) avoids the drawbacks stemming from the poor reliability of absence data by comparing the ecological profile of the sites where the species was observed with that of the whole reference area. Only presence data, therefore, are required.

The study area is divided in a lattice of adjacent cells (quadrats), each being characterized by a series of N eco-geographical variables (EGV). A factor analysis is then performed, which extracts N independent axes. The first one is the “marginality” axis, i.e. the linear combination of original variables on which the species average value mostly differs from that of the global distribution. The other ones are “specialization” axes, i.e. linear combinations of original EGVs on which the species distribution shows the lowest variance relative to that of the global distribution. Overall species marginality and specialization summarize axes values. Most of the relevant ecological information is normally accounted for by a few of the first axes, from which ENFA computes, for each cell, a habitat suitability value ranging from 0 to 100 %. Validation is then performed by comparing the habitat suitability value of a validation subset (presence cells not used for model calibration) with that of random cells. Further details on ENFA mathematical procedures can be found in (Hirzel et al., in press), and the program can be freely downloaded at <http://unil.ch/biomapper>.

6.3.2. Landscape data

I restricted my analysis to the area comprised between the French border at the north-west, and the 500 m isohypse at the south-east (Figure 1.1), as historical data indicate that the species never occurred below this altitude. Including lowland areas in my analysis would have conferred undue importance to land-use categories (such as intensive corn field or thickets) that are totally irrelevant to capercaillie habitat choice. The south-western part of the area (below the middle line on Figure 1.1; $n = 96961$ cells), where most of the remaining populations are to be found, was used for both calibration and validation. I also used the north-eastern part ($n = 71992$ cells), where most populations disappeared during the last two decades (a few birds are still found in small residual patches), as a second, independent validation subset.

Topographical characteristics (altitude, slope and exposure) as well as land-use data for each hectare in the study area were obtained from the Swiss Federal Office of Statistics (Geostat database). From the 74 land-use categories defined in this database, 34 could be dropped, being either not represented in the study area, or irrelevant for assessing capercaillie habitat (e.g. vineyards, orchards). Land-use databases attribute each hectare to a single category, according to a regular sampling. These boolean variables were transformed into quantitative ones by calculating the proportion of hectares from each of these 40 categories within a 1 km^2 circle centred on the focal hectare (a surface corresponding to capercaillie habitat range). Elevation and slope were directly obtained as quantitative variables, but exposure had to be transformed using sine and cosine functions. As several studies suggested disturbing effects of roads on capercaillie (Leclercq, 1985; Ménoni and Bougerol, 1993), I added information on road network, obtained from the Federal Office of Topography (Vector25 database). Potential winter disturbance sources rising from leisure activities, i.e. nordic ski trail (Ménoni et al., 1994), alpine ski trail (Leclercq, 1985), skilifts (Brenot et al., 1996), snowshoes trails (Ménoni, 1994) and sled dogs trails, were also added. Trails and skilifts locations were issued from 1: 25 000 maps edited by the Association vaudoise du tourisme pédestre and the tourist offices from the Vallée de Joux, St-Cergue and Les Rasses. Data were rasterized by computing the closest distance from the focal hectare to any road and every winter leisure activity. I expected some influence of winter wild boar hunting on capercaillie distribution (see : Lefranc, 1987). A layer was built from the mean number of wild boars killed per 100 ha forest, assigned to the 51 hunting regions (Service Forêts-Faune-Nature, unpublished data).

The complete data set for the overall area thus comprised 43 layers in raster format of 1 ha pixel size, referenced to the plane projection of the Swiss coordinate system. Data conversion were performed using Mapinfo professional, and rasterization with Idrisi32. Habitat suitability maps were built for 1) topographical data (4 layers), 2) disturbance data (15 layers), 3) land use data (18 layers), 4) all previous categories (43 layers).

I also used of botanical survey from the Service Forêts-Faune-Nature for the south-western part of the area only (Atlas Phyto-Vaud database). Botanical data were collected on 1 plot per 16 ha forest (regular grid sampling of $400 \times 400 \text{ m}$, $n = 3389$ plots). Within a plot, species cover was estimated in a 10 m diameter circle with Braun-Blanquet (1964) codes. I selected 36 species (belonging to one or more of the four vertical strata ; total $n = 56$) that might explain capercaillie distribution and built raster maps of specific coverage. Values for topographical, anthropogenic structures and wild boar hunting (described here above) were extracted at every botanical plot location. EGVs codes are available in Appendix 3.

Plots were expanded to 5 ha pixel size for visualization. Habitat suitability maps were built at botanical plot location for 1) topographical data (4 layers), 2) disturbance data (15 layers), 3) vegetation data (56 layers), 4) all previous uncorrelated categories (66 layers).

6.3.3. Presence data

Field sampling procedures for presence data are described in Chapter 1. This presence data set was introduced into a GIS and produced a boolean map of capercaillie presence, with pixels (1 ha) taking a value of one if at least one bird sign was attested on it during the field research period (presence cell), and zero otherwise. The set of presence cells from the calibration area (south-western part) was then divided equally into a calibration and a validation set, through a random process in which each presence cell had a 50 % probability of belonging to either the calibration or the validation set.

For the north-eastern part (above the grey line on Figure 1.1), I relied on information gathered by wildlife rangers over the last two decades to localize quasi-extinct local demes.

6.4. Habitat suitability maps for Vaud and Neuchâtel estates

My database eventually consisted of 1161 presence signs for the 1995-2000 period. Droppings were the most frequent signs (73.8 %) followed by sightings (16.6 %) and footprints (6.9 %). Feathers were only rarely discovered (2.7 %). Presence signs were assigned to 1 ha pixels while multiple detections within a pixel were accounted for one presence. Then the rasterized database consists in 783 presence cells divided in 393 cells for the calibration set and 390 cells for the validation set. The second, independent validation dataset encompass 57 presence cells in the north-eastern part of the study area and was used to validate the HS map built with topographical, disturbance and land-use features.

6.4.1. Topography

This habitat suitability map based on four layers explains 89.9 % of total variance with the two first factors (Table 6.1, Figure 6.1a). Overall marginality is moderate (0.56) and capercaillie habitat suitability largely increases with elevation (score 0.99) while exposure (-0.1) and slope (-0.04) have weak contributions. Specialization is moderate (2.17) and mainly associated with slope (0.93). Model validation is moderate with 70.8 % of validation cells having a probability larger than 50 % to be correctly assigned by the model. This differs highly significantly from the 20.2 % obtained for cells randomly chosen from the global distribution (bootstrap test, $p < 0.0001$).

Table 6.1. Scores values for the two first factors (out of four) and four topographical EGVs included into ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor (78.7%)	Specialisation factor 1 (11.2%)
EXPSIN	-0.1	-0.23
SLOPE	-0.04	0.93
EXPCOS	0.06	-0.29
ELEV	0.99	0.04

6.4.2. Disturbance

With 15 input layers and six factors retained, 82.7 % of total variance is explained by the model (Table 6.2, Figure 6.1b). Capercaillie selects distinct areas from global available features (0.82). Increasing distance to large roads (category 1 : 0.36 ; category 2 : 0.51) and to snowshoe trails (0.25) have a positive impact on capercaillie habitat suitability as well as low buildings frequency (-0.32). Surprisingly, capercaillie habitat suitability does not decrease in the vicinity of nordic ski trails (-0.44) and wild boar hunting has a very low influence (0.04). Areas with strong disturbance are avoided as specialization factor (2.01) indicates a rather narrow tolerance. Specialization is mostly accounted for by the frequency of farms, buildings and distance to alpine ski trails. Model quality is good with 82.2 % of validation cells that have a probability larger than 50 % to be correctly assigned, which significantly differs ($p < 0.0001$, bootstrap test) from the 17.1 % expected if cells were randomly chosen from the global distribution.

Table 5.2. Scores values for the six first factors (out of 15) of ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor	Specialisation factor				
	(31.6%)	1 (18.5%)	2 (15.1%)	3 (7.4%)	4 (6.1%)	5 (3.9%)
DNORSKI	-0.44	-0.01	-0.18	0.17	-0.09	-0.38
FBUI	-0.32	0.54	0.74	-0.57	0.31	0.02
FROA	-0.26	0.01	0.04	-0.03	0	-0.04
DALPSKI	-0.26	-0.05	-0.58	-0.25	0.3	0.65
DSLEDOG	-0.18	-0.02	-0.11	-0.31	0.03	-0.27
FFAR	-0.15	-0.83	0.22	0.05	0.01	0.09
DROAD5	-0.03	0	0.01	-0.06	-0.06	0.2
WILDBOA	0.04	0.02	-0.04	-0.07	-0.64	0.11
DROAD6	0.06	-0.02	0.02	-0.01	0.02	-0.02
DALLROA	0.09	0	-0.02	0.01	0.04	-0.07
DROAD3	0.11	0.02	0.01	-0.03	0.02	0.03
DROAD4	0.18	-0.01	0	-0.09	0.06	0.15
DSNOSHO	0.25	-0.02	-0.08	-0.43	-0.38	0.28
DROAD1	0.36	-0.03	0.11	-0.5	-0.02	-0.44
DROAD2	0.51	0.1	0.02	0.15	0.49	0.07

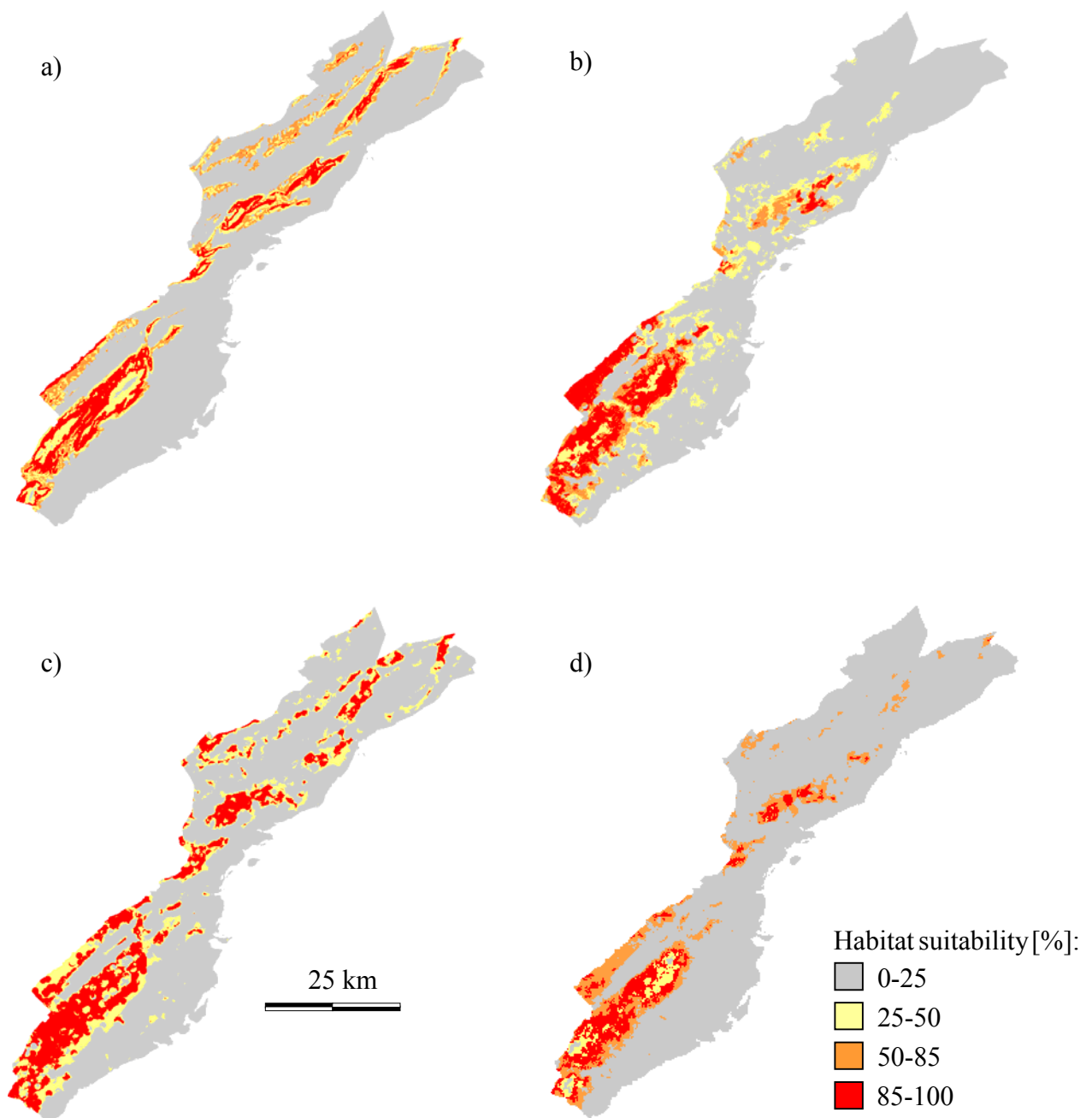


Figure 6.1. Habitat suitability maps for capercaillie in Vaud and Neuchâtel Jura Mts (Switzerland). Maps are built for each 1 ha plot of the area with (a) four topographical EGVs (b) 15 disturbance EGVs (c) 18 land-use EGV (d) Uncorrelated topographical, disturbance and land-use EGVs ($n = 37$).

6.4.3. Land-use

The ENFA is performed on a restricted set of land-use parameters ($n = 18$), excluding land-use parameters related to potential disturbance sources (e.g. farms, roads). Model accounts for 90.1 % of total variance with five retained factors (Table 6.3, Figure 6.1c). Capercaillie prefers areas that differ from global available features (0.80) and is largely favoured by the frequency of open forest (0.46), normal forest (0.27), tree groups (0.23) and devastated forest (0.16). Habitat suitability is damped by the frequency of arable fields (-0.48), other meadows (-0.47), sparse trees (-0.28) and small woods (-0.16). Moderate specialization factor (2.87) is mainly linked to the frequency of arable fields and other meadows. Model validation is moderate with 72.5 % of validation cells that have a probability larger than 50 % to be correctly assigned by the model, which significantly differs ($p < 0.0001$, bootstrap test) from the 17.6 % expected if cells were randomly chosen from the global distribution.

Table 6.3. Scores values for the five first factors (out of 18) of ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor	Specialisation factor			
	(70.8%)	1 (7.9%)	2 (5%)	3 (3.6%)	4 (2.8%)
FARAMEA	-0.48	-0.73	-0.01	0.24	-0.42
FUNPMEA	-0.47	0.64	0.11	-0.11	-0.17
FTHICK	-0.28	0.01	0.11	-0.09	-0.06
FSMAFOR	-0.16	0	0	0.04	0.01
FMARSH	-0.09	0.09	-0.91	0.09	0.02
FWOOARE	-0.09	-0.04	-0.02	-0.02	-0.03
FAFFOR	-0.04	-0.05	-0.03	0.03	0.03
FSHRLAN	-0.01	0.01	-0.01	0.03	-0.04
FBUSALP	-0.01	0	-0.02	-0.01	-0.02
FROCK	0.04	0	0.02	0.03	-0.07
FSMAFOR	0.06	0.11	0.28	0.62	0.43
FROCKALP	0.14	0	0	0.02	-0.05
FRIVBORD	0.15	0	-0.01	0	-0.01
FALP	0.15	-0.02	-0.06	0.09	-0.2
FDEVFOR	0.16	-0.04	0	0.02	0.01
FISOTREE	0.23	-0.15	-0.21	-0.62	-0.54
FFOR	0.27	-0.08	0.09	0.35	-0.51
FOPEFOR	0.46	0.03	0.02	0.09	-0.05

6.4.4. Topography, disturbance and land-use

The first factor (out of 37) displayed a very high marginality value (0.97), showing that capercaillie habitats are clearly distinct from the average habitat available in the study area. The variables favouring capercaillie occurrence (Appendix 4) are elevation (score 0.38), frequency of clear forests (0.31), distance to roads (0.26) and frequency of normal forests (0.18). Negative effects are mostly correlated with the frequency of arable fields (-0.33), other fields (-0.32), frequency of buildings (-0.23), thickets (-0.19), and roads (-0.19). Distance to nordic ski trails (-0.31) may not decrease habitat suitability. Exposure, slope and wild boar hunting have low scores, and thus do not seem to affect capercaillie habitat choice. Specialization was moderate (the overall value of specialization = 2.70 means that presence cells are about 3 times less dispersed than random cells in the ecological space), and mostly

associated with elevation, arable fields, buildings and farms. The four first factors accounted for 71.7 % of specialization (Appendix 4), and the seven first factors for 81.6 %.

Based on these seven first factors, a habitat suitability map was built (Figure 6.1d). This map identifies four large (> 50 ha), high-quality areas for capercaillie, with suitability indices exceeding 0.85. These patches strongly differ in size, the largest ones being located in the south western area. Close to these optimal patches (core areas) are located buffer zones of moderate habitat suitability ($0.5 < p < 0.85$), while the matrix mostly consists of areas either of poor quality ($0.25 < p < 0.5$) or unsuitable ($p < 0.25$).

The validation set defined within the calibration area closely matches the habitat-suitability values predictions of the ENFA. The suitability values predicted for this set exceed markedly those provided for the global set (Figure 6.2). Within this validation set, for instance, 84 % of cells have an habitat-suitability coefficient exceeding 50. This differs highly significantly from the 18.3 % obtained for cells randomly chosen from the global distribution (bootstrap test, $p < 0.0001$).

As for the validation defined outside the calibration area (Figure 6.1d), 87.5 % of cells have an habitat-suitability coefficient exceeding 50, which significantly differs (bootstrap test, $p < 0.0001$) from the 21.7 % expected if cells were randomly chosen from the global distribution. This result also suggests that the extracted factors are indeed good descriptors of capercaillie's habitat in the Jura Mountains.

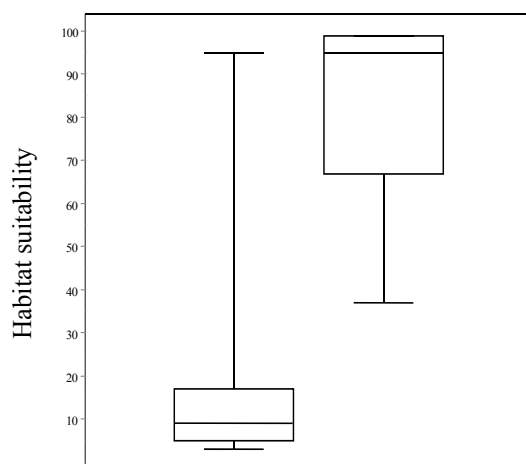


Figure 6.2. Distribution of habitat suitability value for the whole study area (left) and the validation subset (right) encompassing 390 capercaillie presence cells, used only for model evaluation. Boxes delimit interquartile range, middle line represents the median value and whiskers encompass the 80 % confidence interval.

6.5. Habitat suitability maps for Vaud estate

6.5.1. Topography

With four topographical layers, the habitat suitability map based on two retained factors accounts for 86.8 % of total variance (Table 6.4, Figure 6.3a). Capercaillie exhibits a moderate marginality (0.53) and rather selects areas that differ from study site topography. Habitat suitability is mainly influenced by elevation (0.97) and slope (-0.18), while exposure has a weak influence (-0.13). Moderate specialization (1.89) is mostly explained by slope.

Model performances are very good with 91.1 % of validation cells that have a probability larger than 50 % to be correctly assigned by the model. This differs highly significantly from the 39.8 % obtained for cells randomly chosen from the global distribution (bootstrap test, $p < 0.0001$).

Table 6.4. Scores values for the two first factors (out of four) and four topographical EGVs included into ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor (74.7%)	Specialisation factor 1 (12.1%)
SLOPE	-0.18	0.95
EXPSIN	-0.13	-0.26
EXPCOS	0.06	-0.06
ELEV	0.97	0.14

6.5.2. Disturbance

The habitat suitability map obtained with 15 layers and two retained factors accounts for 93.3% of total variance, which is high (Table 6.5, Figure 6.3b). Capercaillie habitats are clearly distinct from global available features (0.7). Distance to roads (category 1 : 0.45 ; category 2 : 0.59 ; category 4 : 0.25), and distance to snowshoe trails (0.22) positively affect habitat suitability. The strong, negative influence of wild boar hunting (-0.31) indicates that capercaillie prefers areas with wild boar hunting pressure below the mean for the study area. Once again, capercaillie habitat suitability do not decrease in the vicinity of nordic ski trails (-0.29). The very high specialization factor (5.13) accounts for a very narrow tolerance towards disturbance range, mainly associated with the frequency of buildings, farms and wild boar hunting pressure. Model quality is moderate : among the validation cells, 67.2 % have a probability larger than 50 % to be correctly assigned by the model, which significantly differs ($p < 0.0001$, bootstrap test) from the 21.2 % expected if cells were randomly chosen from the global distribution.

Table 6.5. Scores values for the two first factors (out of 15) of ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor (81.0%)	Specialisation factor 1 (12.4%)
WILDBOA	-0.31	0.13
DNORSKI	-0.29	0.07
FROA	-0.19	0.03
FBUI	-0.18	-0.96
FFAR	-0.1	0.18
DSLEDOG	0	0.03
DROA5	0.04	0.02
FALPSKI	0.07	0
DROA6	0.15	0
DROA3	0.16	-0.01
DALLROA	0.19	-0.02
DSNOSHO	0.22	0.02
DROA4	0.25	-0.02
DROA1	0.45	-0.05
DROA2	0.59	-0.1

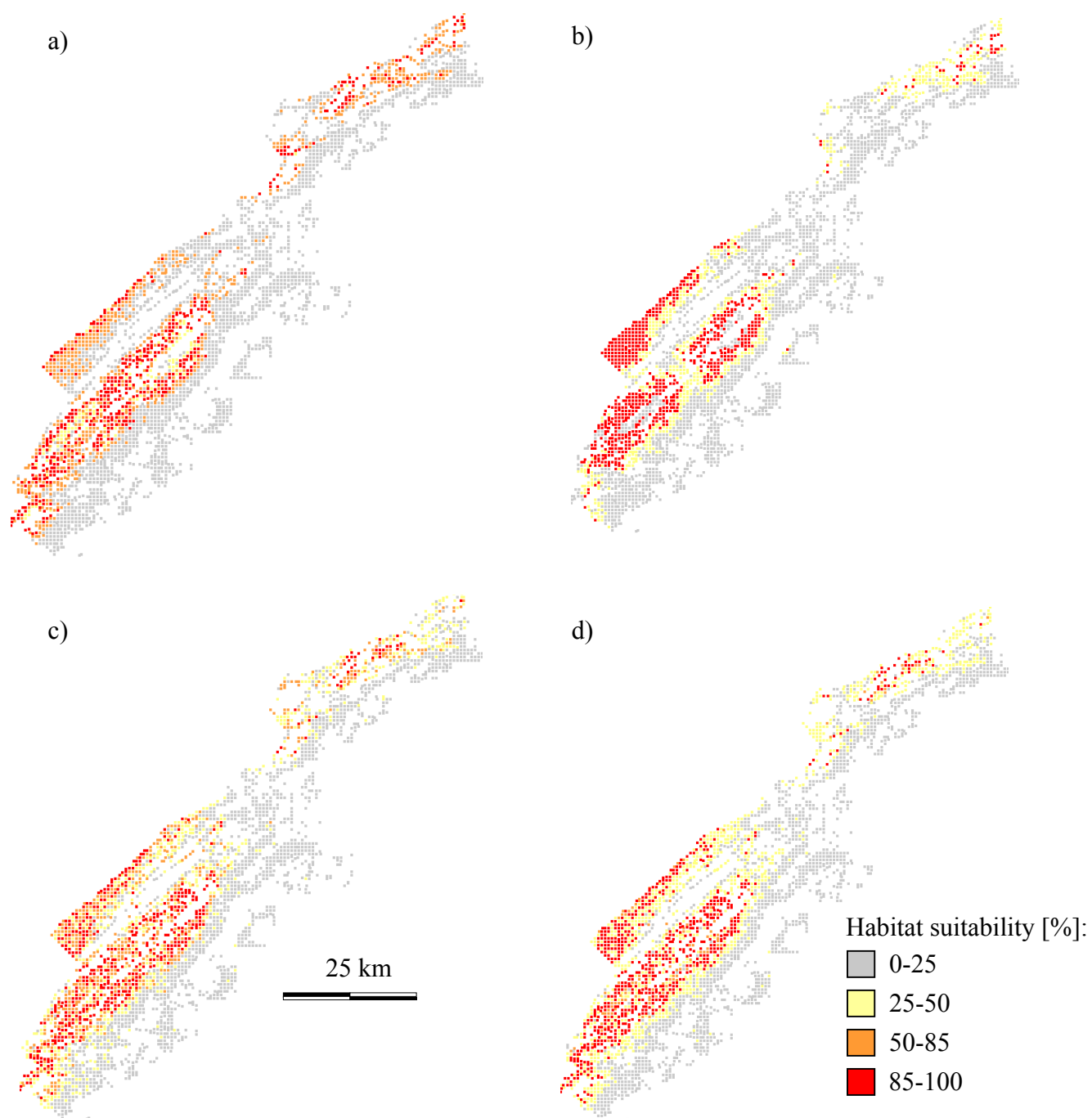


Figure 6.3. Habitat suitability maps for capercaillie in Vaud Jura Mts (Switzerland). Maps built for each vegetation plot ($n = 3389$) of the area with (a) four topographical EGVs (b) 15 disturbance EGVs (c) 56 vegetation EGVs (d) Uncorrelated topographical, disturbance and land-use EGVs ($n = 66$).

6.5.3. Vegetation

A high percentage of total variance is explained by the model (92.2 %) with 56 layers and only two factors (Appendix 5, Figure 6.3c). Capercaillie selects habitats that strongly differed from global available features (0.94). Habitat suitability is enhanced mostly by the cover of bilberry (0.27), cowberry (*Vaccinium vitis-idaea*) (0.27), small cow-wheat (*Melampyrum sylvaticum*) (0.25), white butterbur (*Petasites albus*) (0.24), adenostyle (*Adenostyle alliariae*) (0.23) and from the cover of some understory species such as dwarf-medlar whitebeam (*Sorbus chamaemespilus*) (0.26) and rowan (*Sorbus aucuparia*) (0.21). Capercaillie does not seem to select areas with different undercanopy (0) and raspberry (*Rubus idaeus*) (0.03) covers by comparison the global distribution of these EGVs. Negative factors are mostly correlated with canopy cover (-0.22) and beech cover (-0.19). Capercaillie has a narrow tolerance towards the range of variation of vegetation EGVs, as attested by the elevated specialization factor (4.68). Specialization is mainly associated with herbaceous and understory laburnum covers. Model validation is good: 81.9 % of the validation cells have a probability larger than 50 % to be correctly assigned. This significantly differs from the 31.5 % expected if cells were randomly chosen from the global distribution.

6.5.4. Topography, disturbance and vegetation

During factor extraction, nine variables were further dropped, being either invariant within the calibration set, or linear combinations of other variables. The ENFA performed on 66 layers accounts for 87.2 % of total variance with seven factors retained (Appendix 6, Figure 6.3d). Capercaillie selects habitats that strongly differ from global available features (0.98). Capercaillie occurrence is mostly favoured by elevation (0.29), ericaceous plants : bilberry (0.24), cowberry (0.24), understory plants : dwarf-medlar whitebeam (0.24), small cow-wheat (0.22), and tall grass components : white butterbur (0.22), adenostyle (0.21). Distance to sled dog trails, undercanopy cover, raspberry cover, slope and exposure weakly affect capercaillie habitat suitability, as attested by their low marginality scores. Main negative factors include canopy cover (-0.2), beech cover (-0.17) and fly honeysuckle (*Lonicera xylosteum*) cover (-0.15) and some EGVs related to human disturbance: areas with intensive wild boar hunting were more suitable than hunting reserves or areas with fewer wild boar culled (0.16). By contrast, suitable areas are located closer to nordic ski trails than global distance to nordic ski trails (-0.15). Capercaillie has narrow preferences towards the range of EGV values as attested by the moderate specialization factor (3.26). This specialization was mostly associated with buildings, dog's mercury (*Mercurialis perennis*), farms, dog-rose (*Rosa canina*) frequencies along with distance to alpine ski trails.

The habitat suitability map based on these seven first factors (Figure 6.3d) identifies three high-quality areas for capercaillie, with suitability indices exceeding 0.85. These patches strongly differ in size, the largest ones being located in the south-western area. Close to these optimal patches (core areas) are located buffer zones of moderate habitat suitability ($50 < p < 85$), while the matrix mostly consists of areas either of poor quality ($25 < p < 50$) or unsuitable ($p < 25$).

Model performances are good with 70.1 % of validation cells that have a probability larger than 50 % to be correctly assigned by the model. Suitability values predicted for the validation set are largely greater from the global set (Figure 6.4) and differs highly significantly from the 23 % obtained for cells randomly chosen from the global distribution ($p < 0.0001$, bootstrap test).

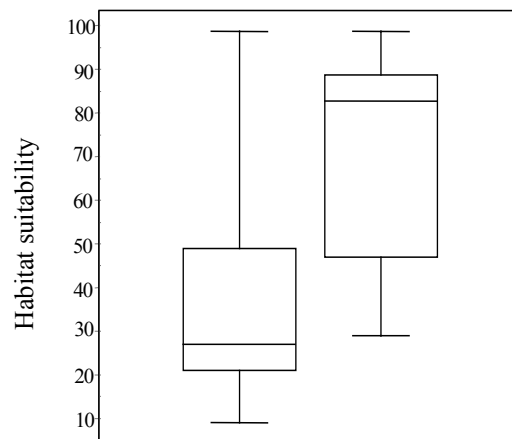


Figure 6.4. Distribution of habitat suitability value for the whole study area (left) and the validation subset (right) ($n = 271$ capercaillie presence cells, used only for model evaluation). Boxes delimit interquartile range, middle line represents the median value and whiskers encompass the 80 % confidence interval.

6.6. Discussion

6.6.1. Models assumptions and limitations

The results of any habitat-suitability analysis are bound to depend on the set of *a priori* assumptions made when collecting and analysing raw data (Baillie et al., 2000; Manel et al., 2000). Assumptions had to be made along the three main steps of the analysis: delimitation of the study area, sampling strategy (in particular with respect to spatial level), and analytical techniques (Aberg et al., 2000 ; Manel et al., 1999; Pettifor et al., 2000).

Our study areas were delimited by the French border for practical reasons (data availability for eco-geographical variables), and by the 500 m isohypse for ecological reasons. As already pointed out, the inclusion of intensive agricultural landscape in the study would have conferred undue importance to totally irrelevant land-use categories, and would have attributed still higher marginality and specialization coefficients to capercaillie. Excluding lowland areas thus allows focusing the study on more relevant aspects of habitat choice. The 500 m limit is obviously disputable, as our marginality axis still evidenced an important role for elevation within the study area, but was chosen for being the lowest elevation at which the species had been mentioned historically (Leclercq, 1987b).

The sampling strategy is obviously of major importance when examining species-habitat relationships (e.g. Rotenberry and Wiens, 1980). The choice of a spatial scale in particular necessarily results from a trade off. Too small a scale, on the one hand, requires huge field efforts to collect data, and may introduce noise (grain irrelevant for habitat choice) and pseudo-replication (many occurrences from the same individual bird; see : Aberg et al., 2000). Too large a scale, on the other hand, may result in a failure to detect relevant landscape heterogeneity (Laymon and Barrett, 1986) and habitat selection (Manel et al., 2000; Sanchez-Zapata and Calvo, 1999). The hectare turned out to be very convenient both in terms of field sampling and habitat use by capercaillie. Home ranges have sizes of about 100 ha (Ménoni, 1991), i.e. 100 sampling units. This scale is thus likely to account for most of the relevant heterogeneity. The 0.04 ha plots (10 m radius) is the smallest scale available in my databases

(Atlas Phyto-Vaud). This scale could have been inadequate (too small to account for most heterogeneity) for capercaillie but intensive, regular sampling over a large area reduced this effect and accounted for most habitat types and botanical features. It is also worth noting that habitat structure in the Jura forests is diversified enough to allow capercaillie to spend both summer and winter within the same territory (Leclercq, 1987a).

Regarding analytical techniques, finally, my choice of ENFA (over regression approaches) allows to avoid biases stemming from poor and / or unreliable absence data. It also avoids having to resort to the “expert opinions” normally required by regression approaches (Austin et al., 1984; Guisan and Zimmermann, 2000). Indeed, standard stepwise analyses performed to select significant EGVs from the original set turn out to be highly sensitive to the algorithms chosen, as well as to the input order. Consequences are that 1) many trials are needed in order to sort out the “best” model, and 2) variables that bear a causal relationship to the focal species’ presence might well be lost in the process, if other EGVs present spurious correlations (Guisan et al., 1999). This implies some subjective choices, and requires a good *a priori* knowledge of the focal species’ ecology. In contrast, ENFA does not reject any input EGV, but only weights them. The subjective components and *a priori* knowledge required are thereby kept minimal (Hirzel et al., in press).

6.6.2. Marginality and specialization scores

The marginality factor (Table 6.3) underlines the preference of capercaillie for open forests. These are defined in Geostat database as having a canopy cover limited to 20-60 % while tree cover in normal forests exceed 60 %. Clear forests in the study area also show abundant, diversified ground vegetation, with bilberry and others ericaceous shrubs in nutrient poor soils (Vittoz, 1998). Bilberry, an essential component of capercaillie diet in summer time, optimally grows in forests with canopy cover around 50 % (Rolstad and Wegge, 1987a; Storch, 1993a).

Elevation was also shown to contribute largely to capercaillie marginality in my study areas (Table 6.3, Appendix 6). From historical information on the process of decline in the Jura Mountains, low-altitude localities were abandoned first (Leclercq, 1987b). This pattern may actually apply to most central, western and south-eastern Europe, where remaining capercaillie populations are presently restricted to mountain forests (Storch, 2000). This trend may result from changes in the structure or composition of low-altitude forests, but also from increasing perturbation levels resulting from their proximity to human settlements.

The detrimental effect of human activity is evident from the negative coefficient attributed to the frequency of meadows, thickets, buildings and farms. The habitat fragmentation that characterizes ruderal landscapes, where original forests are reduced to mere thickets separating meadows, is clearly detrimental to capercaillie (Gjerde and Wegge, 1989; Helle et al., 1994; Lindén and Pasanen, 1987). Conflicts also arise because some forests, otherwise suitable for capercaillie, are industrially logged, or attractive for outdoor recreationists. Repeated disturbances force hens to abandon their clutches, reduce chick survival, and drastically increase winter mortality (Leclercq, 1985; Ménoni et al., 1994; Storch, 1991; Wegge et al., 1990). In the Jura Mountains, Leclercq (1987a) reported lek desertion but also wintering areas desertion after settlements of buildings, parkings and skilifts. Roads may have contrasting effects. Structurally, roads offer favourable elements, including gravel rich components, borders with a high herbaceous layer and forest edges. But roads also facilitate human interspersions into forests for exploitation or leisure activities. In the present instance,

the negative effects seem to predominate, and roads certainly constitute a major indirect source of disturbance.

Although several studies reported breeding and wintering sites desertion in the vicinity of nordic ski trails (Brenot et al., 1996; Leclercq, 1985; Ménoni et al., 1994), this EGV does not appear to reduce habitat suitability in the Swiss Jura Mountains. There, most trails are located in open pastures above 1000 m, close to capercaillie habitats but usually not inside suitable capercaillie forests. As already suggested for some Pyrenean populations (Ménoni, 1994), nordic ski trails may have low detrimental effects as long as they do not coincide with breeding and wintering sites. Moreover, behavioural responses of capercaillie towards human disturbance vary greatly by the type, timing and position of the disturbance (Leclercq, 1985) and intraspecific variation could also occurred. Thus, moderate, regular disturbance sources are sometimes tolerated by capercaillie (e.g. alpine skilifts (Glayre and Magnenat, 1984), nordic ski (this study)).

The effect of winter wild boar hunting on habitat suitability is ambivalent. Strong wild boar presence in Jura capercaillie sites is a recent event (< 20 years) and induces predation on nests and chicks (Lefranc, 1987; Ménoni et al., 1994). A reduced number of wild boars should favour reproductive success but it also implicates hunting performed by people and trained dogs that in turn induce disturbance. My results denoted no clear effect: according to study site delineation and EGVs included in the model, marginality scores indicate that wild boar hunting could be a major disturbance source, have no effect or increases habitat suitability. More acute estimations of wild boar densities and hunters frequentation are further needed to assess the real influence of this factor on habitat suitability.

Bilberry, cowberry, dwarf-medlar whitebeam, small cow-wheat, white butterbur and adenostyle covers positively influence the marginality factor. During the snow free season, capercaillie essentially feeds in the herbaceous layer, with a clear preference for bilberry buds, flowers, leaves and seeds (Jacob, 1987, 1988). High availability of bilberry allows birds to minimize movements in search of food and cover and thus results both in reduced home range size and predation risk (Storch, 1993a). White butterbur and adenostyle also provide cover but seldomly occur in capercaillie diet (Jacob, 1988) perhaps because flowers or seeds are inaccessible for capercaillie. Cowberry, dwarf-medlar whitebeam and small cow-wheat are frequent in the diet of Jura capercaillie during summer and are among favourite food items (Jacob, 1988). Raspberry has a very low marginality score and is not an essential component of capercaillie habitat. But its presence as replacement food could be determinant in areas with low bilberry coverage (Leclercq, 1987a).

My results emphasize the negative influence of strong canopy and beech covers on the marginality factor. Capercaillie prefers moderate canopy covers around 50 % (Storch, 1993b), which allow luxurious ground vegetation growth. Higher canopy closure (around 80 %) could be used in winter, mostly by hens (Storch, 1993b; Devau, 1987). At that time, ground vegetation is snow-covered and hens' arboreal way of life (Gjerde et al., 1985) and preferred food items (see: Jacob, 1988) are not incompatible with strong canopy closures. Dense canopy cover could also be advantageous in terms of protection from wind (and thus minimize energy expenditure) and from predators (Storch, 1993b). Beech buds are eaten by both sexes during spring (Jacob, 1988) while canopy beech (but also sycamore and sometimes coniferous trees) are night roost sites (Leclercq, 1987a). Beech distribution and abundance strongly increase during the last century, as a result of decreasing beech exploitation and warmer climatical conditions. Before 1900, beech was confined to altitude below 1100 m but now, beech is a

regular host of forests up to 1400 m (Dändliker et al., 1993). Its dominant presence in capercaillie habitats negatively modifies forest structure and composition and thus alters habitat suitability.

Though capercaillie showed a marked preference for 10-20° slopes and east exposures in the Alps and Pyrenees, (Ménoni, 1991; Storch, 1993a), my results did not evidence such a preference. Leclercq (1987a) also found a random distribution with respect to slope. In the Bavarian Alps, preference for east exposures coincided with high bilberry availability and was probably an artefact due to bilberry distribution (Storch, 1993c). This lack of selectivity is presumably related to the gentle topography of the Jura Mts. Numerous small hills alternate with flat areas, in sharp contrast with the marked topography of central Alps and Pyrenees.

6.6.3. Habitat suitability map and management options

Habitat suitability maps including topography, disturbance and land-use or vegetation data are based on the seven first factors produced by the ENFA analysis accounts for most of the relevant information gathered on capercaillie in the study area (respectively : 100 % of marginality and 81.6 % of total specialization and 100 % of marginality and 87.2 % of total specialization). Accordingly, capercaillie occurrence at the landscape level is very adequately predicted. The single large patch of high-quality habitat that constitutes the south-western part of the study area indeed shelters the core of remnant populations. Moreover, large proportions (respectively : 84 % and 70.1 %) of presence data from the validation set were attributed suitability scores exceeding 50. Finally, presence data outside the calibration area (north-eastern part of the study area) were remarkably well predicted by this analysis.

It is worth pointing out that these once-occupied localities, together with other patches which appear favourable but presently devoid of capercaillie, are characterized by a marginal localization and / or fragmented structure. Small and marginal patches certainly suffer from increased perturbation rates, owing to human activity and occasional excursions from generalist predators (Leclercq et al., 1997). Furthermore, small patches are more heavily affected by demographic stochasticity (Foley, 1994). Capercaillie populations from highly fragmented boreal forests have been shown to be more prone to extinction than less fragmented populations with similar habitat quality (Rolstad and Wegge, 1987b). Finally, the largest unoccupied forest patches are localized nearby large capercaillie populations (e.g. Mont Sâla, Grand Risoux region). These observations point to the importance of maintaining suitable habitats in areas with large forest availability.

In this respect, the most obvious target for management that emerges from my analysis, appears to be the Mont Risoux (Figures 6.1 & 6.3). This single large forest patch in the western part of the study area, close to the French border, is furthermore connected with similar habitat in France (Catusse et al., 1991). From my analysis, however, its suitability appears to be intermediate, and presence data, accordingly, are scarce. Information from lek counts (Sachot et al., in press) and wildlife rangers indicate that local density dramatically dropped over the last decade. The main reason for this trend apparently lies in the progressive closing of the forest (Dändliker et al., 1993; Ménoni, 1994). Preliminary sensitivity analyses indeed indicate that an increase in the frequency of clear forests might be enough to significantly boost the suitability of this patch. I therefore strongly recommend that the efforts forest managers a ready to furnish should focus on this patch, with the goal of clearing the existing structure by a moderate and differentiated timber harvest.

A second target, the Mont Sâla region (Figures 6.1 & 6.3) is of prime importance because it shelters the largest number of capercaillie (around 70 adults in 2001) and is the largest patch. This region located in the south-western part of the study area has highly suitable cells but also cells of moderate quality (50 - 85). Nonetheless, capercaillie numbers are decreasing, with different intensities according to leks locations (Sachot et al., in press). Large abundance reduction mainly occurs in moderate quality patches. As for the Mont Risoux, progressive forest closure is involved, but also human disturbance linked to leisure activities (Dändliker et al., 1993). In this patch, future management plans should focus on the maintenance of extensive silviculture in good quality cells while forests of moderate quality should be preferentially selectively cut and forestry roads closed to public traffic.

Though the present study is restricted to a geographically limited area and a very specific question, I think that the methodology I apply is readily expandable to address similar questions in different contexts from conservation biology. In connection with sensitivity analyses of habitat suitability, ecological-niche factor analyses have the potential to provide a valuable generalized tool for land managers and conservation biologists.

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Capercaillie management in a human-induced landscape, the Jura Mountains

7

7.1. Abstract

1. Capercaillie abundance has seriously declined during the last century over most of its distribution range. In Switzerland, protection and habitat conservation for this endangered bird have been locally funded. Several management strategies have been proposed but their relative effects on capercaillie persistence is largely unknown.
2. I developed a new software (Patcher) linking habitat suitability maps with metapopulation viability analysis and explore detailed management scenarios for the Swiss Jura capercaillie populations.
3. The patch recognition algorithm implemented in Patcher identifies eight capercaillie populations in the Swiss Jura Mountains, which corresponds to main areas with capercaillie presence. Two areas with a single breeding pair are not recognized because of their now low habitat suitability.
4. Simulations, performed on the whole metapopulation (31 populations) without management, predict a substantial extinction risk (14.8 %) over the next century.
5. Comparison of several management scenarios points out an important limitation of modelling. Beyond variables distribution ranges for a study site, extrapolations cannot be performed. It prevents to test management scenarios with larger amount of important habitat features than observed in the field.

7.2. Introduction

Conservation of the endangered capercaillie is a preoccupying issue in the management of forests resources in most central and occidental European populations (Storch, 2000). Since 1988, the Swiss Agency for the Environment, Forests and Landscape and the Swiss Ornithological Institute improved the protection of the capercaillie in Switzerland and released financial support for silvicultural practices that would improve its habitat conditions. In western Switzerland, some land-managers and foresters have recently applied habitat enhancements for capercaillie. Positive effects on capercaillie populations have not been yet recorded, perhaps because patches were too small (< 50 ha) or far from existent capercaillie populations. Thus, detailed investigations on location, size and effects of additional habitat enhancements at the metapopulation level become necessary.

In this chapter, I use the habitat suitability map built on Chapter 6 and link it to TetrasPool, the spatially, age-structured and stochastic metapopulation model based on capercaillie life cycle developed in Chapters 2 & 3. With these procedures, the aim is to rank detailed management scenarios for capercaillie.

7.3. Methods

7.3.1 Overview

My capercaillie model is structured in three major parts, briefly described here. First, a spatially explicit habitat suitability (HS) map is built on capercaillie observations and geographic information system (GIS) databases. Second, the HS map is derived to a patch structure, exported to TetrasPool. Finally, the PVA model is run to test and rank management options.

7.3.2 Habitat suitability map

The analysis was restricted to the area comprised between the French border at the north-west, and the 500 m isohypse at the south-east (Figure 1.1), as historical data indicate that the species never occurred below this altitude (Leclercq, 1987b). Topographical characteristics ($n = 4$), land-use data ($n = 18$) and potential winter disturbance sources rising from leisure activities ($n = 15$) were used to build a capercaillie habitat suitability map with the ecological niche factor analysis or ENFA (Hirzel et al., in press). For further details on study site delimitation, mathematical procedures and ENFA parameterisation, refer to Chapter 6.

7.3.3 Link between HS map and PVA model

Species perception of habitat quality and fragmentation determines populations' location and carrying capacity (Roloff and Haufler, 1997; Wilson et al., 1998). Therefore, a program called Patcher (Sachot, 2001) was built that defines patches, based on the following considerations:

- 1) A *habitat quality threshold* is defined as the lowest habitat quality for which habitat is still suitable for the species. Identifying a habitat quality threshold for a species with complex life-history traits (i.e. several habitat types for reproduction, summer life and winter life) is not straightforward. Ideally, threshold should be set on the relationship between population

fitness (such as fecundity and survival) and habitat quality estimators (Roloff and Haufler, 1997). But the exact shape of the fitness-habitat quality relationship has been addressed only by a few studies and it remains largely unknown for most species. Nonetheless, habitat quality threshold could be subjectively inferred from studies that quantified home range size and fitness indicators (e.g. Roloff and Haufler, 1997) or chosen as either the smallest HS value for the least exigent life-history trait of the species or as a fixed percentage of HS values at observation points (Akçakaya and Altwood, 1997).

2) A habitat *quantity threshold* is defined as the minimum area below which an individual cannot perform its entire life-cycle. This threshold erases small patches that do not fit species-area requirements.

3) A *neighbourhood distance* between habitat cells grouping suitable cells and delineating patch boundaries. It could be the foraging distance or the distance between summer and winter sites of the species. For a focal patch, suitable cells separated by a distance equal or smaller to species movements' capacities are grouped within the same patch. Cells further apart are assigned to different patches.

4) The link between HS patch map and population carrying capacity (K) is achieved by a user-defined function. This function weights home range size according to total patch HS value and scaled K . For example, given two same-sized patches, the patch with the highest total HS value will allow species to have smaller home range sizes and have a larger K than the less suitable patch.

7.3.4 HS-PVA link parametrization

Capercaillie preferentially used cells with HS value greater than 50 (Figure 6.2, Chapter 6) so that the habitat quality threshold was set at 50. The habitat quantity threshold was fixed to 100 ha which corresponds to the minimum home range size recorded for a female capercaillie in the Bavarian Alps (Storch, 1993). In central Europe, hens do not use distinct seasonal ranges and mean movement distance between seasons is $0.8 \text{ km} \pm 0.3$ ($n = 7$) (Storch, 1995). The neighbourhood distance was thus set to eight cells. This corresponds to the assumption that suitable cells within 800 meters of each other belong to the same patch.

A linear negative relationship was assumed between total patch HS value and home range size. Capercaillie home range size largely differs between season and sites. In Europe, home range sizes recorded for hens in very good habitats is around 100 ha (Storch, 1993; Wegge and Rolstad, 1986). In medium quality habitats, mean home range size was 519 ± 355 ha (Storch, 1993). Home ranges overlap over 50 %, so that 50 ha spring home range was used for $HS = 100$ and 260 ha for $HS = 50$. Using a linear interpolation, mean home range size for each population (h_i) is obtained by:

$$h_i = -(21/5) \cdot \frac{\sum_{i=1}^n HS}{n_i} + 470$$

where HS is the value of habitat suitability and n_i the number pixels in population (i). Population carrying capacity (K_i) is given by $K_i = n_i / h_i$. It can be verified that in optimal habitats, minimal home range size (without overlap) is 50 ha ($= -(21/5) \cdot 100 + 470$) and 260 ha for medium-quality habitats.

7.3.5 PVA model

Population viability analyses were performed using TetrasPool (Sachot, 2000), a software based on the life-cycle of grouse with a spring breeding period, autumn dispersal of offspring and winter mortality. The model combines a metapopulation structure with demographic data on capercaillie. Most of the life-history parameter values used in my simulations (means and standard deviations) stem from a long-term field study (1976-1999) of a French Jura populations (Table 4.1). Original data and details of the collecting methods were obtained from B. Leclercq (1987a, c). When no local information was available (data on dispersal and home ranges), I used values from the literature on other west-European populations instead (Ménoni, 1991; Storch, 1993; Wegge et al., 1981). For further details on mathematical procedures and model parametrization, refer to Chapters 3 & 4.

7.3.6 Ranking management options

I performed PVAs for the whole metapopulation (Figure 7.1) but developed scenarios for the Swiss part only, to guide future managements in this country. I did not build scenarios for the French populations as various, large-scale forest managements have already been realized in the French part of the Jura Mts between 1990-2000 and none will be funded in France in the near future. All simulations included both demographic and environmental stochasticity and consisted of 1000 replicates run over 100 years.

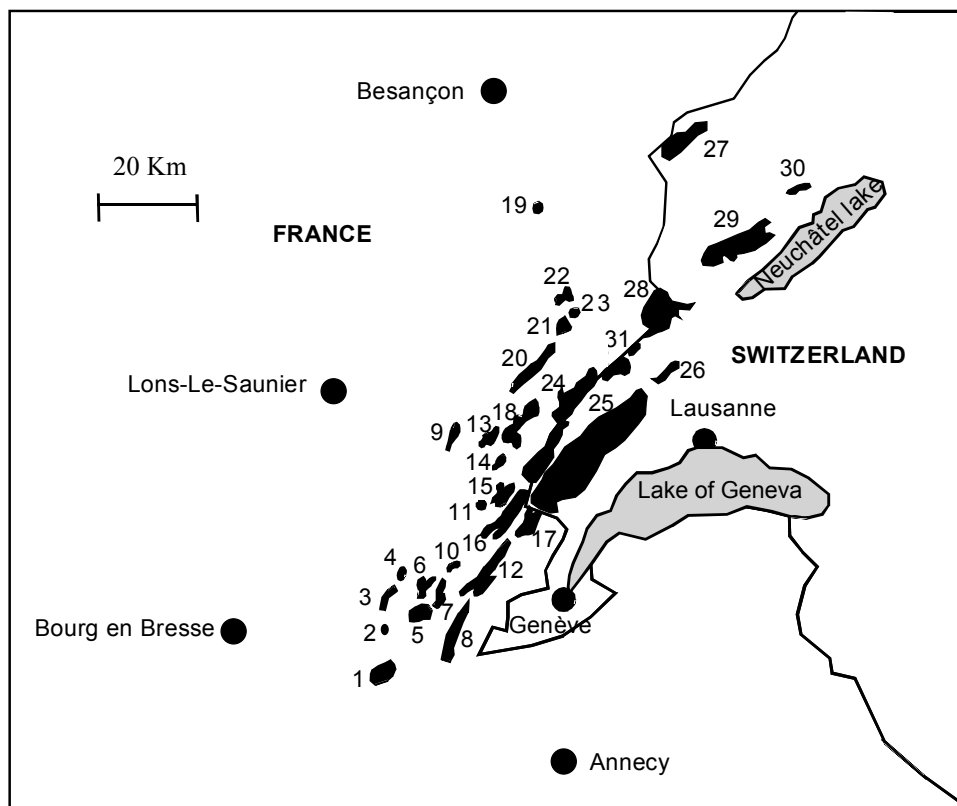


Figure 7.1. Location of the 31 capercaillie populations in the Jura Mts identified from (Montadert and Chamouton, 1997) in France and from the patch-recognition algorithm of habitat suitability map in Switzerland.

Scenario 1

Metapopulation extinction risk was estimated with default life-history values together with the habitat map built without habitat enhancement. Scenario 1 represents the baseline to which other management options will be compared.

Scenario 2

The purpose of scenario 2 and subsequent was to examine the probable benefits of human-induced and natural forested habitat changes with various geographic dispositions. In scenario 2.1 dense forest was converted to open forest over 7183 ha punctually distributed in areas with HS greater than 25. The effect of less intensive management was investigated in scenario 2.2. This scenario follows scenarios 2.1. but management was realized over 3592 ha only. In scenario 2.3, dense forest was converted to open forest in seven new patches (mean size = 1182 ha \pm 324.8 ha) close to present capercaillie populations. As capercaillie could inhabit habitat generated by catastrophes, I designated a scenario 2.4 relying on catastrophes. Cyclones and storms largely varied in timing, position and extent with a mean area of 245.7 ha \pm 240.5 ($n = 7$; Groupe Lothar, unpublished data). In scenario 2.4, I randomly selected 246 ha of forested areas with HS greater than 25 and converted them into devastated forest.



Figure 7.2. Location of scenario 2.1 (medium grey), scenario 2.2 (dark grey), scenario 2.3 (black lines) and scenario 2.4 (black).

Scenario 3

Field survey indicated that capercaillie avoids roads, particularly during autumn (Leclercq, 1985). Thus, in scenario 3 road layers of category 4 and 5 were closed in all Swiss Jura forests with a few exceptions. Access to farms, restaurants and main viewpoints were maintained. This scenario is credible because the Swiss law (Lfo, October 4th 1991, Art.15) supports forest road closure.

Scenario 4

The negative influence of nordic ski structures on capercaillie habitat suitability and survival was frequently reported (Brenot et al., 1996; Ménoni, 1994b). In scenario 4, I moved nordic ski trails crossing forests with HS greater than 50 to the nearest opened areas (i.e. alpage, meadow, grassland) or closed them if opened areas were not available in the vicinity (< 1 km) of actual ski trails.

Scenario 5

The effect of wild boar hunting is ambiguous. Wild boar destroys capercaillie clutches and broods and thus should be maintained at low levels (Lefranc, 1987; Ménoni, 1994a). On the other hand, wild boar hunting is an additional disturbance source during winter that reduce capercaillie survival rate (Chapter 6). In scenario 5, I incorporated a new network of three game reserves of 2260 ha, 3233 ha and 2136 ha sizes (Figure 7.3). These reserves were centralized on core capercaillie habitats and there, wild boar hunting was not allowed. The aim of scenario 3, 4 and 5 was to assess the relative benefits of human disturbance reduction on habitat suitability and capercaillie persistence.

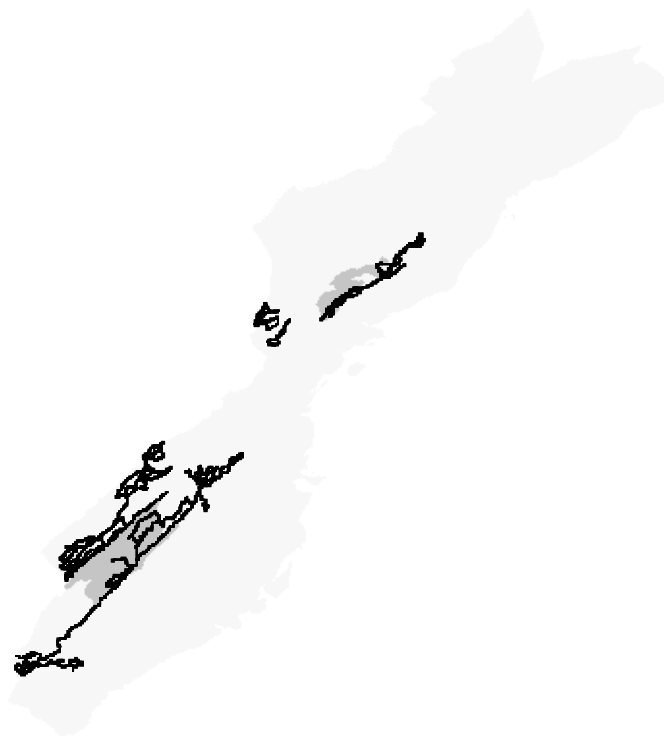


Figure 7.3. Location of maintained nordic ski trails (black) and wild boar hunting reserves (medium grey).

Scenario 6

The purpose of scenario 6 and subsequent was to examine the effects of several cooperative approaches between forest users and their relative effects on capercaillie persistence. Scenario 6.1 is a pure forestry scenario that combines forest roads closure (scenario 3) with dense forest conversion into clear forest over 7183 ha (scenario 2.1). Scenario 6.2 results from cooperation between hunters and foresters. This scenario combines a reduced wild boar hunting (scenario 5) and dense forest conversion into clear forest over 3592 ha (scenario 2.2). Scenario 6.3 is a cooperative approach between tourist offices and hunters because it accounts for a reorientation of nordic ski trails (scenario 4) and a reduced wild boar hunting (scenario 5). Finally, I designed the very optimistic scenario 6.4 where all forest partners cooperate. This scenario includes forest roads closure (scenario 3), nordic ski trails reorientation (scenario 4), reduced wild boar hunting (scenario 5), dense forest conversion into clear forest over 7183 ha (scenario 2.1) and cyclones and storms over 246 ha (scenario 2.4).

7.4. Results

7.4.1 Patch structure

The patch recognition algorithm implemented in Patcher identified eight capercaillie populations in the Swiss Jura Mts, which exactly correspond to main areas with capercaillie presence (Figure 7.4). Among these, six populations are located in the canton de Vaud and two in the canton of Neuchâtel. Largest populations (n° 24, 25) are located at the south-western part of the study area. Moderate and small-sized populations are distributed at the north-east. Two areas with a single pair of capercaillie were not recognized by the algorithm. These regions located at the extreme north-east of the study site have a too moderate habitat suitability to be identified by the algorithm. French Jura populations' numbers and locations are given in Figure 7.1.

Carrying capacities were calculated in two different ways. For the eight Swiss patches, they were inferred from the patch-recognition algorithm (see above). For French populations ($n = 23$), carrying capacities were evaluated by dividing the population area by the net capercaillie home range in optimal areas (50 ha). This gives an optimistic estimation of populations carrying capacities in France. For populations located at the border between Switzerland and France (n° 24, 28, 31), final carrying capacities were obtained by summing K inferred from Patcher for the Swiss area with expert K obtained in the French area.

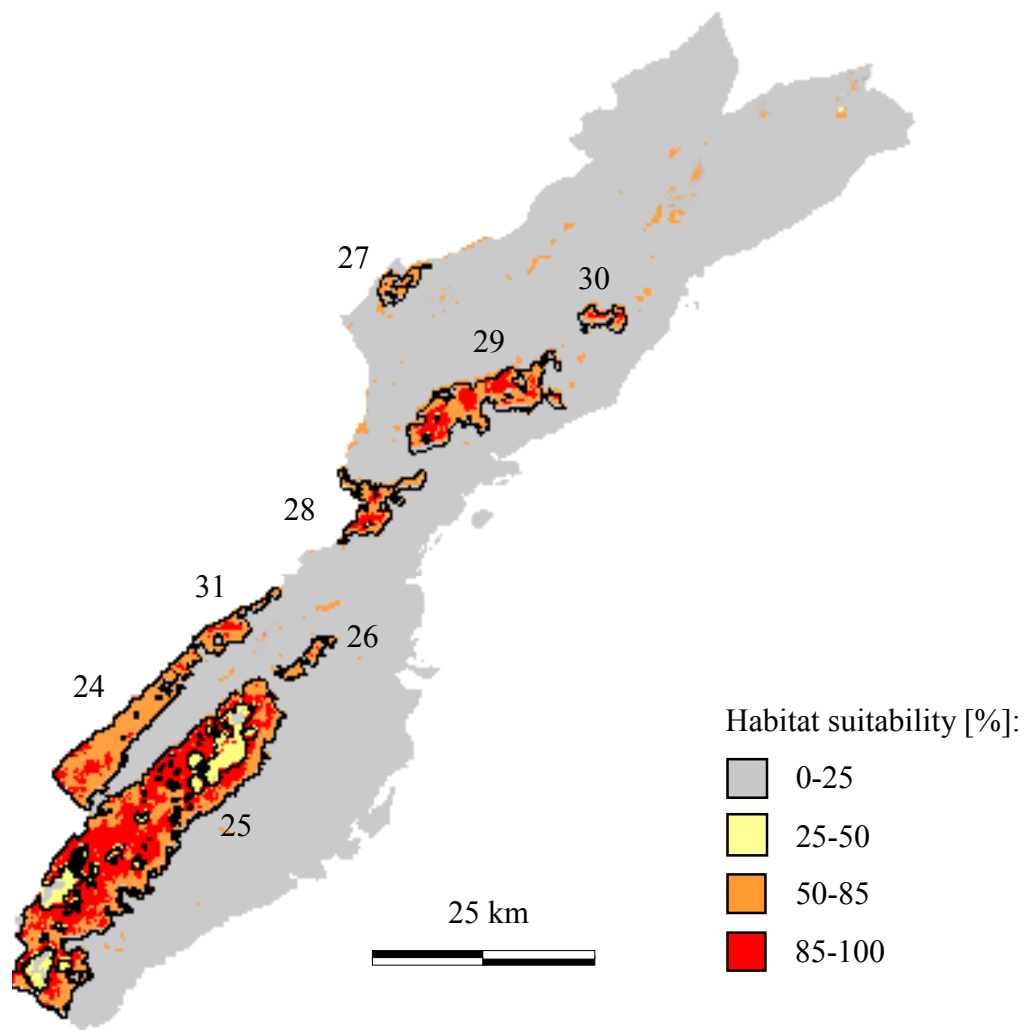


Figure 7.4. Habitat suitability map without habitat enhancement and locations of the eight capercaillie populations in the Swiss Jura Mts. Black : populations delineation by the patch-recognition algorithm with a habitat quality threshold of 50, a 800 m neighborhood distance and a 100 ha habitat quantity threshold.

7.4.2 Metapopulation dynamics

For scenario 1, a moderate value of extinction probability (14.8 %) and a median time to extinction of 89 years (for extinct runs) were recorded over the next 100 years. During the simulated time horizon, a global decrease in bird abundance was predicted (Figure 7.5). After 100 years, predicted capercaillie abundance was very low and about 25.9 ± 30.7 for the overall Jura Mts. Figure 7.6 presents extinction time for every populations within the next 100 years. Small populations (n° 2, 4, 9, 19, 23, 26, 27, 30, 31) are doomed to extinction and capercaillie loss in these areas is rapid, with median times to extinction < 10 years. The above results were obtained with a null abundance threshold for all populations. Metapopulation risk of decline is also largely conditioned by the abundance threshold at which populations are assumed to be extinct (Figure 7.7). Extinction drastically increases for higher threshold. For example, an abundance threshold of 50 individuals boosted extinction probability to 84.4 %.

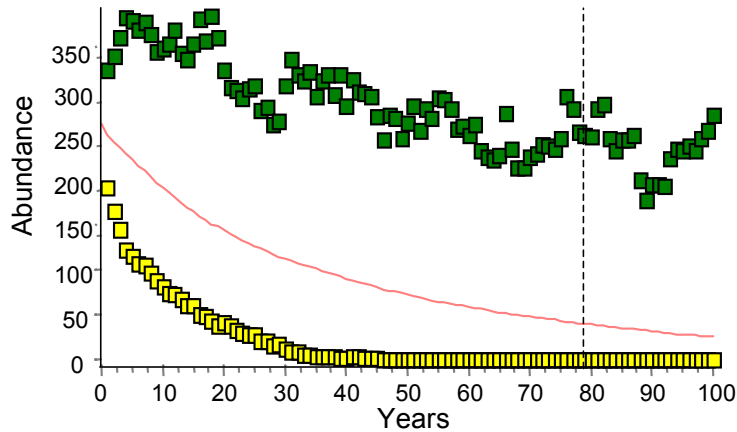


Figure 7.5. Trajectories for scenario 1, without management. Dark carrel : highest abundance recorded for a replicate, Grey carrel : smallest abundance recorded for a replicate. The vertical dotted line represents the median time of extinction. Each curve is based on a simulation with 1000 replications.

Scenarios aimed at improving habitat conditions with conversion of dense forest towards more opened structures showed a positive impact on extinction risk. However, the results obtained seemed somewhat paradoxical and counterintuitive. Scenario 2.1 that converts large proportions (7183 ha) of dense forest into forest with moderate canopy cover was, surprisingly not the most efficient ($P(ext) = 13.2$, $T(ext) = 89$). The less extreme forest management that converted half of this area (3592 ha) into clear forests (scenario 2.2) appeared more efficient ($P(ext) = 13.8$, $T(ext) = 89$). Due to these counterintuitive outcomes, simulations were stopped at this stage in order to detect possible causes for the odd behaviour (see discussion).

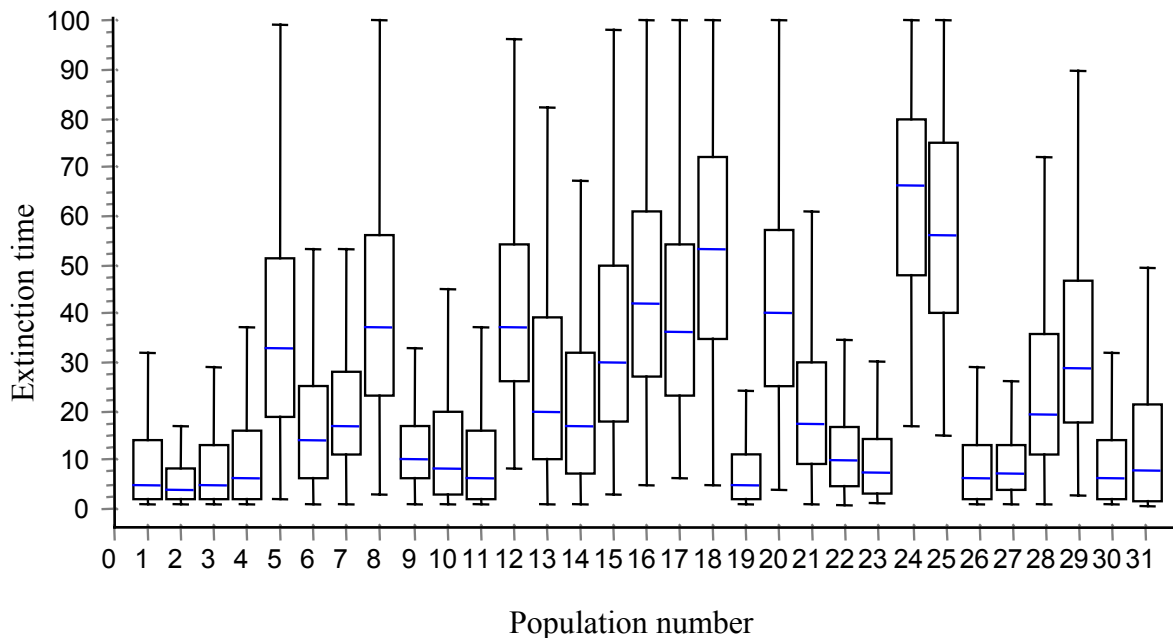


Figure 7.6. Plots showing the distribution of extinction time for Scenario 1. Boxes encompass the range of values between 25 % and 75 % quartiles, and the central line represents the median. Bars encompass the range of values between the 25 % quartile minus 1.5 times the difference between the quartiles 75 % and 25 % and the 75 % quartile plus 1.5 times the difference between the quartiles 75 % and 25 %. Plots are based on 1000 replications over 100 years.

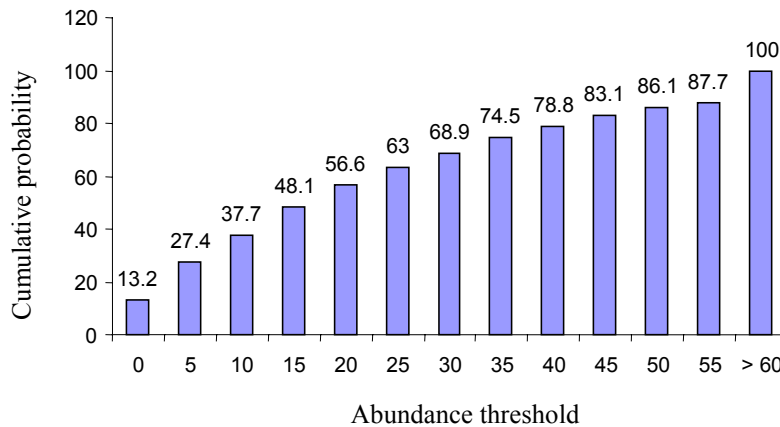


Figure 7.7. Cumulative extinction probability of scenario 1 for 13 abundance thresholds. Distributions are based on 1000 replications over 100 years.

7.5. Discussion

7.5.1. Efficiency of Patcher, the patch-recognition algorithm

The patch-recognition algorithm accurately delineated actual capercaillie patches, except for two small patches with a single breeding pair. There are two possible explanations for this. First, habitat suitability in those marginal sites might be explained by locally important factors that have a low score in my analysis because they were not representative for all other populations. Second, the size of these populations is too small to be recognized by the algorithm as a result of historical artefact. There is currently a single pair of breeding birds at each site, but they may have started breeding there when habitat quality was much higher. They have not left the patch, although habitat quality is now below that of other populations.

7.5.2. Capercaillie persistence without habitat management

The identified patch structure was introduced into the PVA model thus furnishing a link between habitat suitability maps at the landscape level and demographic data on population dynamics. In scenario 1 without habitat enhancement, a moderate extinction probability (14.8 %) was recorded for the 31 capercaillie populations identified. This level is roughly similar to the level obtained with 35 populations delineated by expert opinion (10.4 %). However, increasing the extinction threshold drastically boosted extinction risk to higher values. This quasi-extinction risk is a way to approximate Allee effects (Burgman et al., 1993), a decrease in population viability at low abundances. For capercaillie, Allee effect might be produced by several, interacting factors such as difficulties to find a mate at low densities (Legendre et al., 1999), sex-differentiated chicks survival (Wegge, 1980) and genetic diversity loss (Bouzat et al., 1997). The exact shape and importance of Allee effect remain largely unknown for capercaillie. Nonetheless, I do not expect a linear, monotonic decline to extinction but an accelerated decline to extinction at low densities (Allee effect) as already attested short before capercaillie population extinction in central Europe (Dändliker et al., 1993; Klaus, 1994).

In scenario 1, extinction probabilities and median times to extinction strongly vary according to populations. This can be explained by a source-sink dynamics: large populations produce numerous of immigrants going to less stable, more extinction prone populations. In small populations, extinctions result from demographic stochasticity and Allee effect. The predicted median time to extinction of 89 years is similar to quarter-time needed for coniferous trees seeds to attain the size and structure suitable for capercaillie in mountain habitats. Waiting on natural regeneration to compensate habitat loss and offer suitable habitats is dangerous. Meanwhile, capercaillie populations will certainly fall to very low levels or be already extinct. Forest management of established forests then becomes a necessity.

7.5.3 The limits of ENFA as a tool to investigate management scenarios

Results of initial simulations quickly revealed counterintuitive outcomes: large-scale forestry management was less efficient than small-scale management. This seems paradoxical because large, positive marginality scores for these variables attested of their positive impact on capercaillie habitat suitability. Problem lies in the way habitat suitability is calculated in the present version of ENFA. The suitability score of each cell is computed from a count of all cells with species presence that lay as far or farther apart from the median than the focal cell on a factor axis (Hirzel et al., in press). For each factor, the median value represents the highest suitability value ($HS = 100$) and is the optimum value for this factor. Cells further on the left or on the right tail of the distribution have smaller suitabilities. This method is certainly valid as long as the optimum lies within the range of values investigated. If however the optimum lies outside the range, so that HS actually increases or decreases monotonically, then any attempt to extrapolate is doomed to failure (Figure 7.8).

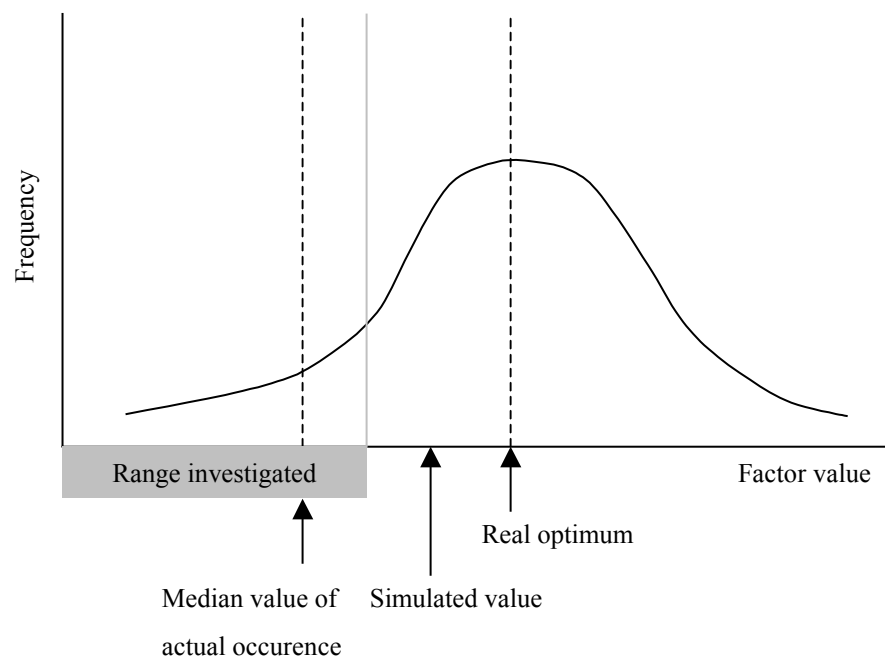


Figure 7.8. Species distribution for a factor with a real optimum value outside investigated range. Within the study area, a local optimum exists and is calculated as the median value. Simulated values outside this range will be classified as having a $HS = 0$ by ENFA, because no observed presence lays as far or farther apart from the median.

The actual distribution of capercaillie presence on « normal forest » factor and even more evidently on « clear forest » factor, strongly suggests that this problem is happening (Figures 7.9 & 7.10). The ratio of presence cells / global cells monotonically increases from the left end (class = 0) to the right end (class = 1.1; Figure 7.10), strongly suggesting that the next class (1.2) should be still better. However, a pixel within this class will be classified as having a HS = 0 by ENFA, simply because no observed presence lays as far or farther apart from the median (Figure 7.8).

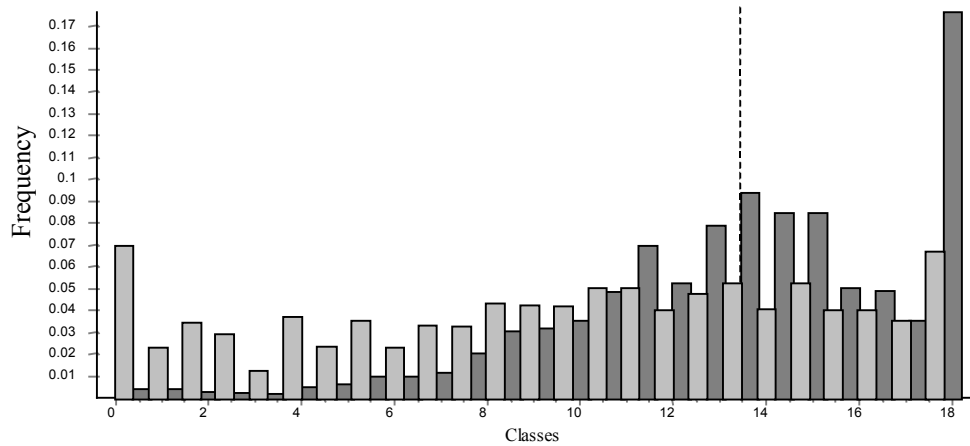


Figure 7.9. Global and species distributions on the « normal forest » factor. Classes indicate pixels value in a 1 km radius after normalisation. Light grey: global cells, dark grey: species cells distribution. The dotted line indicates median value for the species distribution.

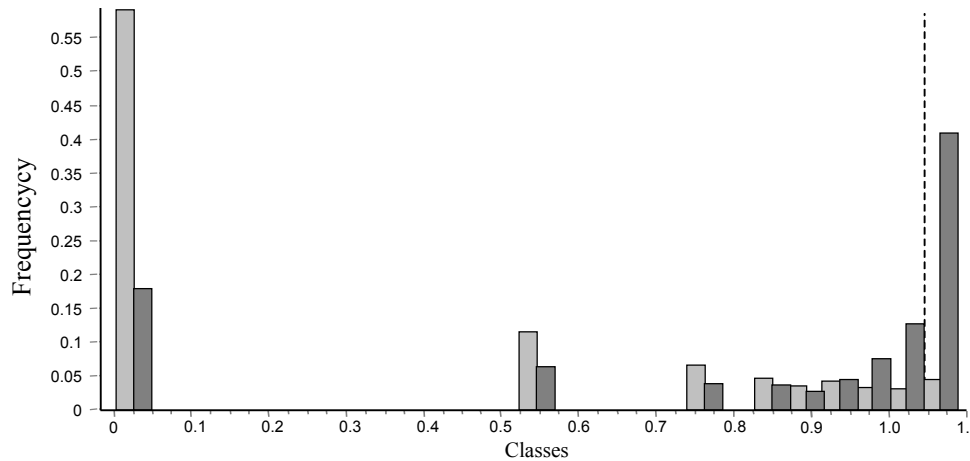


Figure 7.10. Global and species distributions on the « clear forest » factor. Classes indicate pixels value in a 1 km radius after normalisation. Light grey: global cells, dark grey: species cells distribution. The dotted line indicates median value for the species distribution.

The straightforward conclusion is that ENFA should be restricted to interpolations, i.e. HS calculations within the same range, and not to extrapolations outside primitive range. This limitation is also valuable for all other multidimensional statistical methods. Models are established on observed species preferences within a study site, thus site-specific optimum values exist for all factors. Elsewhere, other optimum values could exist. For example, the Jura capercaillie preference for an open / normal habitat mixture does not correspond to most optimal conditions for the bird because in the boreal zone, highest capercaillie numbers were

recorded in large areas with old, open forest (Wegge and Rolstad, 1986). Such positive relationship between open forest and capercaillie can be expected from Figure 7.10. Capercaillie uses low classes less than available but has increasing preferences for higher classes and open forest presence as attested by the very skewed species distribution. The median optimum value does not reflect this.

Other ways to circumvent the problem might be 1) to infer suitability from the ratio of presence / global cells 2) to restrict investigations to scenarios transforming cells of the 0 class to the observed median value. Outside the range investigated, species distribution cannot be established, partly because no simple, linear predictions exist.

7.5.4 Other limitations of landscape-PVA modelling

This chapter represents the first exploration of habitat suitability-PVA modelling for capercaillie with highly detailed management scenarios. Similar methodologies have already been successfully applied to rank conservation options for small birds (Akçakaya and Altwood, 1997; Akçakaya et al., 1995), and arboreal marsupials (Lindenmayer and Possingham, 1996) with various reserve network implementations or animal translocations. A multitude of scenarios could be envisaged with PVA models, but to keep results as simple as possible, I focused on the most probable scenarios in a central European framework. The more important assumptions and limitations of my investigations are the following:

1) Density dependence at low population densities (Allee effect) certainly exists in capercaillie populations but the lack of data prevents detailed parameterisation. I approximated Allee effect with metapopulation quasi-extinction thresholds that necessarily have arbitrary values. Fixing an extinction threshold depends on whether it is more important not to overestimate or not to underestimate extinction risk (Akçakaya and Altwood, 1997). Here, I prefer not to fix a threshold because this priority-linked decision has important consequences in terms of metapopulation persistence.

2) Several assumptions have been made about carrying capacities. First, habitat quality within populations was assumed constant over 100 years. This is probably not exact because some populations suffered a large decline in carrying capacity during the last century (Leclercq, 1987a). Second, field data linking habitat suitability with capercaillie home range size are sparse. Despite this, I used the few extant data from the literature, as my previous modelling attempts with uniform habitat quality for all patches were unsuccessful to rank management scenarios. Third, carrying capacities were calculated with optimal home range size recorded for capercaillie for the French part of the study area. It probably inflates breeding territories availability (i.e. K) in this country.

3) Scenarios presented in this chapter affect population carrying capacity but not directly life-history parameters. In Chapter 4, I concluded that efficient management options for capercaillie should include both actions on life-history parameters and carrying capacities. Further simulations should account for both an increase in population carrying capacity and life-history parameters.

4) I did not model genetic factors that may substantially decrease small population persistence because data were unavailable for capercaillie.

Given the above assumptions, my population viability analysis is a very optimistic approach. In reality, the Jura Mts capercaillie populations certainly is at higher risk than suggested by my scenarios. This is not unusual because many complex and interacting factors that may influence population dynamics cannot be incorporated into a computer simulation program (Lindenmayer et al., 1993). Although I was unable to identify one best scenario among the above scenario, this approach points on a major multidimensional model restriction linked to variables distribution.

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8.1. Tools for conservation biologists, land-managers and foresters

The endangered capercaillie provides an excellent opportunity to develop new tools and approaches for conservation biologists and land-managers. Conflicting priorities in the land-use and limited resources availability forced those people to propose management options for declining species on *a priori* expectations or with few relevant data. During the thesis, I specifically used and built programs linking a few available field data with statistical models (Table 8.1), thus providing a more comprehensive understanding of capercaillie population ecology. This process will also allow formulating scientifically based management policies. Initially, all analyses used or developed here stem from theoretical biology but were specifically incorporated to allow parameterisation with real field data. This is a significant improvement because theoretical population models usually require high numbers of parameters, which are generally lacking for rare and endangered species.

Table 8.1. Main tools developed or used in the thesis helping conservation biologist, land-managers and foresters. Half dot: already mentioned in the literature but not scientifically validated and / or not used for capercaillie, empty dot: new concept.

<i>Tool</i>	<i>Status</i>	<i>Chapter</i>
TetrasPool, a PVA model to assess grouse persistence and rank management options	○	4
Quantitative estimation by logistic regression of capercaillie winter habitat quality in unknown forest patches	◐	5
Quantitative estimation by logistic regression of hazel grouse winter habitat quality in unknown forest patches	◐	5
GIS and ENFA to build habitat suitability without expert opinion and provide quantitative habitat suitability values at the landscape level	◐	6
Patcher, a patch recognition algorithm to identify and delineate populations from habitat suitability maps	○	7

8.2. From observational data to population viability models

Capercaillie observers remarked a large reduction of displaying capercaillie on leks since the last decades. Statistical analyses performed in Chapter 2 confirmed this view. However, the trends differ according to the population because several factors interact with different intensities between populations. Capercaillie counts on leks is a first step towards understanding the demography of capercaillie. Other informations are necessary to rank the possible causes of population decline and to identify key life-history parameters, in order to focus management options adequately.

With the development of TetrasPool, I propose a software designed to explore population dynamics and identify key life-history parameters at the population level (Chapter 3 & 4). For capercaillie, simulations predict a marked decline and a significant extinction risk (10.4 %)

over the next century. Sensitivity analyses point out an important result: conservation efforts should be focused not only on enhancing adult survival but also on minimizing risks of brood failure and juvenile mortality. Simultaneously, effective conservation would require several actions aimed at improving habitat suitability over large areas independently of the source-sink status.

TetrasPool accounts not only for occupancy-type models but also for spatial structure and differences in local population dynamics. It addresses a much larger spectrum of species and questions than the specific capercaillie decline because of the generality of its implementation. One can deal with all others species with similar life-history patterns distributed in populations throughout the landscape. Model parameterization is reduced to a few, essential demographical variables that can be collected in the field. This software could be used to support various types of decision in conservation biology.

8.3. Habitat selection and regression causes

8.3.1 At the local level

This is the first study to provide a winter-habitat suitability quantification for capercaillie and hazel grouse in their sympatric zone of occurrence (Chapter 5). At the local level, my results point out the main factors affecting these forest-dwelling grouse. I confirmed previous knowledge on forest structure and composition but also highlighted some unknown characteristics (Table 8.2). Both grouse species have different needs in terms of habitat structure and composition and showed no avoidance of moderate human disturbance sources in plots of cooccurrence. Capercaillie preference for moderate canopy closure, low understory cover and fir presence is not brand-new but preference for grazed forest and tolerance towards canalized winter recreational activities were less known. By contrast, hazel grouse avoided grazed forest and strongly preferred young successional stages. There, understory rowan, willow and beech are important food resources while spruce cover provides shelter from predators. Forest patches with inadequate structure or without essential winter food items are unsuitable. Thus, local regressions causes are canopy and undercanopy strong closure as well as feeding trees cutting to favor more precious wood species.

With these local models developments, I palliated the need for objective habitat suitability estimation at the local level. Their simplicity (they are based on five parameters only, which can be easily estimated in the field) combined with high reliability (see: Chapter 5) should help to widenth their use to other areas of sympatry.

8.3.2 At the landscape level

At the landscape level, I brought important contributions in terms of influential factor ranking with ENFA, acute and fiable prediction of capercaillie occurrence with ENFA and habitat suitability map construction (Chapter 6). None of the previous studies on capercaillie ever managed to cope with as many potential factors that may influence habitat suitability and rank them. Capercaillie habitat suitability increases with 1) elevation 2) moderate canopy closure (< 60 %) 3) bilberry cover. High proportions of 1) meadows 2) thickets 3) buildings 4) farms 5) roads largely decrease habitat suitability as well as 6) strong canopy cover and 7) strong beech cover. At this spatial level, habitat loss and fragmentation are of major concern (Table 8.2).

In Chapter 6, I provided a habitat suitability value for every pixel based on ecogeographical variables with statistical models and validated it. Such small-scale map allows the identification of core areas, moderate quality areas and low quality matrix. This habitat modelisation could highlight some temporarily unoccupied but suitable habitats that may play an important role during dispersal. These habitat islands must be conserved and traditional methods issued from expert opinion would certainly failed to identify them. Thus, expert opinion must be confined to build gross models, unless data are insufficient to construct statistical models.

8.4. Impact of detailed habitat management scenarios on metapopulation persistence

The habitat suitability map is a snapshot of landscape suitability for a species at a given time. Linking the habitat suitability map with population viability analysis include a predictive aspect over time and more realism into the model. The explicit use of GIS data into PVA was achieved by Patcher, a software that pin out populations and theirs respective carrying capacities from habitat suitability maps on the basis of biologically meaningful parameters. This patch-recognition algorithm identifies eight capercaillie populations in the Swiss Jura Mts, which corresponds to main areas with capercaillie presence. Two areas with a single breeding pair were not recognized because of their now low habitat suitability. Comparison of several management scenarios points out an important limitation of modelling. Beyond variables distribution ranges for a study site, extrapolations cannot be performed. It prevents to test efficient management scenario with large conversion of habitat features.

8.5. A grouse-adapted management strategy

In central Europe, management concepts have already been suggest for French (Ménoni, 1994; Leclercq, 1987) and German (Storch, 1995, 1999; Suchant, 2001) capercaillie metapopulations as well as for French hazel grouse metapopulations (Montadert et al., 1994). Table 8.2 summarizes earlier recommendations for capercaillie and my thesis results, while Table 8.3 presents a local management strategy for hazel grouse.

Capercaillie has large habitat requirements. A local habitat-suitability increase by forestry practices could favour a subpopulation installed around a lek. But limiting capercaillie management to this local aspect is insufficient for long-term capercaillie persistence. For the above reasons, capercaillie management strategy must involve three spatial levels. First, at the local level (1-100 ha), forest structure and composition as well as low human disturbance are essential (Table 8.2). At the population level (100-1000 ha), a habitat mosaic of various habitat types is determinant. At the landscape level (>1000 ha), forest size and distribution determine capercaillie presence.

For hazel grouse, habitat preferences were determined at the local level in zones of cooccurrence with capercaillie. Theirs habitat requirements are highly different but hazel grouse presence is also determined by habitat structure and composition (Table 8.3). By contrast with capercaillie, human disturbance do not affect hazel grouse occurrence probability. In the field, both grouse species presence could be favored by a patchy distribution of rejuvenation stages within old successional stages.

Table 8.2. Main capercaillie management options at three spatial levels. Full dot: already mentioned in the literature and scientifically validated management practice in central Europe (see: Ménoni, 1994; Leclercq, 1987; Storch, 1995, 1999; Suchant, 2001), half dot: already mentioned but not scientifically validated and / or not used for capercaillie, empty dot: new concept.

<i>Level</i>	<i>Management</i>	<i>Status</i>	<i>Chapters</i>
Local	1-100 ha		
	<i>Structure</i>		
	Vegetation layering	●	5
	Canopy and undercanopy cover between 30-60 %	●	5, 6
	Understory cover around 15 %	◉	5
	Favor group harvest of mature trees	◉	5
	<i>Composition</i>		
	Stimulate fir presence if possible in high proportion at high elevation sites	◉	5
	Maintain and favor strong bilberry cover as well as a rich and diversified	●	4, 5, 6
	Herbaceous layer that provide hide / food for chicks and adults		
Population	<i>Disturbance</i>		
	Avoid human interspersions outside ski trails	◉	5, 6
	Limit access to wintering sites	◉	5
	100-1000 ha		
	Mosaic distribution of habitat types, mainly old successional stages	●	5
	Maintain present cows grazing pressure to ensure the persistence of grazed-forest habitat type	◉	5
	Increase habitat suitability and thus carrying capacity independently of the source / sink status	○	4
	Improve adult survival by limiting access to wintering sites	◉	4
Landscape	Increase breeding success and juvenile survival rate with restricting access to breeding areas	◉	4
	1000 to > 10000 ha		
	Maintain present forest patch structure	●	4
	Keep large forest sizes > 50 ha	●	6
	Limit further forest fragmentation by new roads and ski trails	◉	6
	Reduce forest conversion into farmlands and settlements	◉	6
	Maintain connectivity between patches, distance must not exceed 5-10 km between suitable patches	●	4, 6

Table 8.3. Hazel grouse management at the local level in sympatric areas with capercaillie. Full dot: already mentioned in the literature and scientifically validated management practice in central Europe (see: Montadert et al., 1994), half dot: already mentioned but not scientifically validated and / or not used for hazel grouse (see: Montadert et al., 1994).

<i>Level</i>	<i>Management</i>	<i>Status</i>	<i>Chapter</i>
Local	1-100 ha		
	<i>Structure</i>		
	Vegetation layering	●	5
	Low canopy and undercanopy cover between 30-60 %	●	5
	Understory cover around 50 %	●	5
	Favor group harvest of mature trees and gap-phase rejuvenation	●	5
	<i>Composition</i>		
	Stimulate rowan, willow and beech presence as well as young spruce in high proportion	◉	5
	<i>Disturbance</i>		
	Hazel grouse is not very sensitive towards this factor, no special measure	◉	5

8.6. Future prospects

With the above tools (Table 8.1) we can now address various questions such as 1) management scenarios 2) sizes and disposition of reserve network 3) the effect of corridors 4) translocations and reintroductions, on metapopulation persistence. In fact, resource planning now has a solid framework integrating habitat-based population viability.

Nonetheless, PVA scope and utility could be expanded in several, complementary directions. First, I assumed a constant habitat throughout a simulation. This is probably incorrect because all natural habitats vary. For example, fruits, herbs and insects availability yearly change within a forest patch. Over a century, forest growth modify successional stages and forest structure while over a millennium, global climatic warming could affect tree species composition. In fact, habitat change and habitat loss cause population occupancy reduction and this certainly plays a role for species such as capercaillie. TetrasPool could further be improved by accounting for temporal trends in the carrying capacity. Habitat loss could be integrated by specifying observed habitat loss rates during the last decades that in turn affect the carrying capacity and thus population occupancy.

Second, although density dependence regulation is well understood from a theoretical point of view, its estimation in natural population is generally lacking. My models accounted for a ceiling type of density dependence at high densities but no density dependence was included at low densities. The Allee effect could draw a small population away from the carrying capacity and toward extinction by chance events. It can dramatically change extinction risk and should be considered as a further implementation in TetrasPool.

Third, for both animals and plants, only little information on dispersal exists, which hinders PVA development and further dynamical process understanding. Factors affecting dispersal rate, departure decision, and dispersal paths choice according to landscape structure are not fully understood. Moreover, spatial heterogeneity is a complex phenomena involving patterns or mosaics of habitats at the landscape level that might affect individual movements, species distribution and population persistence. Integration of dispersal in heterogeneous habitats with GIS techniques is now a merging field to be explored. At the same time, field programs monitoring juvenile dispersal rates or adult movements between winter and summer sites on the long term should be initiated. I am very confident that the combination of these species field data with dispersal-dedicated GIS tools are promising research topics.

Finally, demography certainly plays a major role in the short-term persistence of species affected by human activities. Genetic factors might also play a role in managed populations close to extinction owing to the lack of genetic diversity. Low effective populations size is likely to be associated with reduced fitness and reduced opportunities for future adaptative change. Nonetheless, the real contribution of population genetics (level of inbreeding in small populations, genetic variance within and among populations) to population persistence is a largely unexplored domain. Such analyses add a further level of complexity and require more data. Thus, a cooperative approach between field biologists, conservation biologists and genetists become a necessity. Field biologists could thus gain understanding in the observed phenomenas. For conservation biologists, this multi-approach research should allow to build more realistic and efficient models, which may in turn support management decision. Genetists could address unsolved questions such as the propagation of individuals in a landscape and its influence on the measured genetic variance. Moreover, impacts of bottlenecks on population genetics and persistence might be clearly identified and understood.

8.7. Bibliography

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Appendix 1.

Definitions

RF	Proportion of reproductive females
RFSD	Standard deviation in the proportion of reproductive females
NRF_i	Number of reproductive females in population i
F	Fecundity
FSD	Standard deviation in fecundity
SR	Sex ratio
AS	Adult survival rate
ASSD	Standard deviation in adult survival rate
NJ_i	Number of juveniles in population i
JS	Juvenile survival rate
JSSD	Standard deviation in juvenile survival rate
NP	Total number of populations
T	Number of timesteps
R	Number of replicates
ET	Extinction threshold for populations
HR	Female home range size
HRO	Female home range overlap
K_i	Carrying capacity of population i
$N(t)_i$	Initial abundance at time t for population i
D_{ij}	Distance between populations i and j
DD	Average dispersal distance for a juvenile female
DR	Dispersal rate
DRSD	Standard deviation in dispersal rate
PCV	Percentage of common variance between populations
EN_i	Number of emigrant from population i
DP_{ij}	Probability to disperse from population i to population j
R_i	Radius of population i
IN_i	Imigrant number into population i
DPS_i	Standardized dispersal probability for population i
$NJBW_i$	Number of juveniles in population i before winter
ASP_i	Adult survival probability for population i
JSP_i	Juvenile survival probability for population i
NAS_i	Number of adults survivors in population i
NJS_i	Number of juveniles survivors in population i
AHR	Adjusted home range
[Ran3]	Uniform number drawn from a continuous distribution between [0; 1].
Beta1f	Number drawn from a Beta distribution
Bino	Number drawn from a binomial distribution
Poidev	Number drawn from a poisson distribution

Detailed algorithm of TetrasPool

1. Initialisation

- 1.1 User defines life-history parameters, populations and simulation parameters.
- 1.2 Check parameters and values entered.
- 1.3 Prompt user to correct values when necessary.
- 1.4 Initialise parameter values and matrix for simulations and results storage.
- 1.5 Calculate the adjusted home range which is the net territory size and allow population radius (R_i) calculations :

$$AHR = ((HR - (HR \cdot HRO)) / 100)$$

2. Replication

- 2.1 Reset result matrix and extinction time variables to 0.
- 2.2 For each timestep, following steps are repeated :

- 2.2.1 Correlation coefficients are :

$$\text{Sigma} = \text{RFSD} \cdot (\text{PCV} / 100)$$

$$\text{Epsilon} = \text{RFSD} - \text{Sigma}$$

- 2.2.2 If the simulation is performed:

- with environmental correlation, the proportion of reproductive females in each population is affected by the same trial from :
$$\text{RF} = \text{Beta1f}(\text{RF}, \text{Sigma})$$
- without environmental correlation, the proportion of reproductive females is unchanged (RF).

- 2.2.3 For each population, following steps are repeated :

- with environmental stochasticity and environmental correlation, proportion of reproductive females is drawn from :
$$\text{RF}_i = \text{Beta1f}(\text{RF}, \text{Epsilon})$$
- with environmental stochasticity only :
$$\text{RF}_i = \text{Beta1f}(\text{RF}, \text{RFSD})$$
$$\text{F}_i = \text{Beta1f}(\text{F}, \text{FSD})$$
$$\text{DR}_i = \text{Beta1f}(\text{DR}, \text{DRSD})$$
- without environmental stochasticity, the proportion of reproductive females, fecundity and dispersal rate are constant values :
$$\text{RF}_i = \text{RF}$$
$$\text{F}_i = \text{F}$$
$$\text{DR}_i = \text{DR}$$
- with demographic stochasticity, current number of reproductive females and juveniles numbers are issued from :
$$\text{NRF}_i = \sum \text{Bino}(\text{N}_i, \text{RF}_i)$$
$$\text{NJ}_i = \sum \text{Poidev}(\text{F}_i \cdot \text{SR})$$

while number of individuals leaving the source patch are :

$$\text{EN}_i = \sum \text{Bino}(\text{NJ}_i, \text{DR}_i)$$

- without demographic stochasticity, reproductive females, juveniles numbers and emigrant number are rounded values:

$$NRF_i = \text{round}(NRF_i \cdot RF_i)$$

$$NJ_i = \text{round}(NRF_i \cdot F_i \cdot SR)$$

$$EN_i = \text{round}(NJ_i \cdot DR_i)$$

2.2.3.1 Dispersal probability depends on the size, shape and distance of target populations. With circular population patches, radius is :

$$R_j = \sqrt{(K_j) \cdot (AHR \cdot 10000) \cdot (1/\pi)}$$

and the negative exponential dispersal probability function is :

$$DP_{ij} = \arctan((R_j/D_{ij})) \cdot 1/\pi \cdot e^{(-D_{ij}/DD)}$$

2.2.3.2 The number of emigrant within the same population or populations at the carrying capacity is null :

$$\text{if } (i=j) \text{ or } (N_i(t)=K_i) \text{ then } EN_i=0$$

when populations are distinct or under their carrying capacity, emigrant number is calculated by :

$$\text{if } (i < j) \text{ and } (N_i(t) < K_i) \text{ then } EN_i = (NJ_i \cdot DR_i)$$

2.2.3.3 When user selects directional dispersal:

(i) The standardized dispersal probability is:

$$DPS_{ij} = DP_{ij} / \sum DP_{ij}$$

(ii) Dispersers attribution, for every patch and every disperser, a random number is drawn from a uniform distribution :

$$x = [\text{Ran}3]$$

(iii) Target populations (j) are inspected in turn but should be below their carrying capacity to receive a dispersing individual :

$$\text{if } (i < j) \text{ and } (N_j + NJ_j + IN_j - EN_j < K_j)$$

(iv) The random number is compared to the standardized probability and while the condition:

$$x < DPS_{ij}$$

- if this relation is true, another target population is inspected and standardized dispersal probabilities are cumulated for inspected targets :

$$DPS_{ij} = \sum DPS_{ij}$$

- if $x > DPS_{ij}$ then emigrant is assigned to the population j to the last added population j :

$$IN_j = IN_j + 1$$

2.2.3.4 When user selects random dispersal:

(i) The dispersal probability remains the same :

$$DP_{ij} = DP_{ij}$$

(ii) Migrants attribution is done for every patch when populations are below their carrying capacity :

$$\text{if } (i < j) \text{ and } (N_j + NJ_j + IN_j - EN_j < K_j) \text{ then}$$

$$IN_j = \text{round}(DP_{ij} \cdot EN_i)$$

Non-attributed migrants are lost in the matrix of unsuitable habitats and assumed to be dead

2.2.3.5 Stock emigrant and immigrant numbers

2.2.3.6 The number of juveniles before winter is updated :

$$NJBW_i = NJ_i - EN_i + IN_i$$

as well as total population size after dispersal:

$$N_i(t+1) = \text{round}(N_i + NJBW_i)$$

2.2.3.7 Winter survival is then applied and depends on stochasticities involved :

(i) With environmental stochasticity, adult and juvenile survival probabilities are :

$$ASP_i = \text{Beta1f}(AS, ASSD)$$

$$JSP_i = \text{Beta1f}(JS, JSSD)$$

(ii) Without environmental stochasticity, probabilities remain constant values :

$$ASP_i = AS$$

$$JSP_i = JS$$

(iii) With demographic stochasticity, adult and juveniles numbers become :

$$NAS_i = \sum \text{Bino}(N_i, ASP)$$

$$NJS_i = \sum \text{Bino}(NJBW_i, JSP)$$

(iv) Without demographic stochasticity, stage abundances are :

$$NAS_i = \text{round}(N_i \cdot ASP)$$

$$NJS_i = \text{round}(NJBW_i \cdot JSP)$$

(v) Total population size after survival but before threshold or ceiling adjustments is explained by :

$$N_i(t+1) = NJS_i + NAS_i$$

2.2.3.8 Final population and metapopulation sizes depends on the user-defined threshold:

$$\text{if } N_i(t+1) < \text{threshold then } N_i(t+1) = 0$$

2.2.3.9 Population size is adjusted on the carrying capacity:

$$\text{if } N_i(t+1) > K_i \text{ then } N_i(t+1) = K_i$$

2.3 Calculate summary statistics for the timestep and replace :

$$N_i(t) = N_i(t+1)$$

3. Calculate summary statistics for the replication (e.g. extinction risk for population and metapopulation, median time to extinction for population and metapopulation)
4. Calculate summary statistics for the simulation (e.g. $\lambda = (RF \cdot F \cdot SR \cdot JS) + AS$) and store results in matrix and files.

Appendix 2.

Carrying capacity (K) and female abundance (Groupe Tétras Jura, unpublished data; Service Forêts-Faune-Nature, unpublished data) for the 35 capercaillie patches of the Jura Mountains.

Population number	K	Initial abundance (female only)
1	17	1
2	1	1
3	6	1
4	4	1
5	16	7
6	4	2
7	6	6
8	30	13
9	3	3
10	4	1
11	3	1
12	22	30
13	9	3
14	5	2
15	8	7
16	14	12
17	14	12
18	31	16
19	3	1
20	20	12
21	117	64
22	70	25
23	2	1
24	23	3
25	6	3
26	3	2
27	24	6
28	40	12
29	8	4
30	1	1
31	1	1
32	1	1
33	5	1
34	7	7
35	10	4

Appendix 3.

Ecogeographical variables used to predict capercaillie habitat suitability.

Parameter	Code
Elevation (m)	ELEV
Slope (°)	SLOPE
Exposure (°)	
Exposure (sine)	EXPSIN
Exposure (cosine)	EXPCOS
Human disturbance	
Distance to roads (m)	DALLROA
Distance to roads category 1 (size > 6 m)	DROA1
Distance to roads category 2 (4 m < size < 6 m)	DROA2
Distance to roads category 3 (2.5 m < size < 4 m)	DROA3
Distance to roads category 4 (size < 2.5 m, forest road, hard cover)	DROA4
Distance to roads category 5 (size < 2.5 m, forest road, soft cover)	DROA5
Distance to roads category 6 (size < 1 m)	DROA6
Distance to nordic ski trail	DNORSKI
Distance to alpine ski trail	DALPSKI
Distance to sled dogs trail	DSLEDOG
Distance to snowshoe trail	DSNOSHO
% of roads	FROA
% of buildings	FBUI
% of farms	FFAR
Wild boar hunting index	WILDBOA
Land use	
% of alpage	FALP
% of bushy alpage	FBUSALP
% of rocky alpage	FROCKALP
% of shrubs lands	FSHRLAN
% of unproductive meadow	FUNPMEA
% of arable meadow	FARAMEA
% of unproductive grassland	FUNPGRA
% of rocks	FROCK
% of afforested areas	FAFFOR
% of forest islands (size < 0.25 ha)	FSMAFOR
% of thickets	FTHICK
% of wooded areas	FWOOARE
% of open forest	FOPEFOR
% of devastated forest	FDEVFOR
% of forest	FFOR
% of isolated tree group	FISOTREE
% of small forest	FSMAFOR
% of marsh, river and lakes	FMARSH
% of river borders	FRIVBOR
Botanical species	
% of canopy cover	FCANCOV
% of canopy <i>Abies alba</i>	FCABIALB
% of canopy <i>Acer pseudoplatanus</i>	FCACEPSE
% of canopy <i>Fagus sylvatica</i>	FCFAGSIL
% of canopy <i>Picea excelsa</i>	FCPICEXC
% of canopy <i>Sorbus aria</i>	FCSORARI
% of canopy <i>Sorbus aucuparia</i>	FCSORAUC
% of undercanopy	FUNC
% of understory	FUND

% of understory <i>Abies alba</i>	FUABIALB
% of understory <i>Acer pseudoplatanus</i>	FUACEPSE
% of understory <i>Fagus sylvatica</i>	FUFAGSIL
% of understory <i>Laburnum alpinum</i>	FULABALP
% of understory <i>Lonicera nigra</i>	FULONNIG
% of understory <i>Lonicera xylosteum</i>	FULONXYL
% of understory <i>Picea excelsa</i>	FUPICEXC
% of understory <i>Ribes alpinum</i>	FURIBEALP
% of understory <i>Rosa canina</i>	FUROSALP
% of understory <i>Rubus idaeus</i>	FURUBIDA
% of understory <i>Sorbus aria</i>	FUSORARI
% of understory <i>Sorbus aucuparia</i>	FUSORAUC
% of understory <i>Sorbus chamaemespilus</i>	FUSORCHA
% of herbaceous layer	FHER
% of herbaceous <i>Fagus sylvatica</i>	FHFAGSIL
% of herbaceous <i>Abies alba</i>	FHABIALB
% of herbaceous <i>Acer pseudoplatanus</i>	FHACEPSE
% of herbaceous <i>Adenostyles alliariae</i>	FHADEALL
% of herbaceous <i>Athyrium filix-femina</i>	FHATHFIL
% of herbaceous <i>Calamagrostis varia</i>	FHCALVAR
% of herbaceous <i>Cardamine heptaphylla</i>	FHCARHEP
% of herbaceous <i>Cardamine pentaphyllos</i>	FHCARPEN
% of herbaceous <i>Carduus defloratus</i>	FHCARDEF
% of herbaceous <i>Deschampsia caespitosa</i>	FHDESCAE
% of herbaceous <i>Dryopteris filix-mas</i>	FHDRYFIL
% of herbaceous <i>Elymus europaeus</i>	DHELYEUR
% of herbaceous <i>Epilobium angustifolium</i>	FHEPIANG
% of herbaceous <i>Festuca altissima</i>	FHFESALT
% of herbaceous <i>Gentiana lutea</i>	FHGENLUT
% of herbaceous <i>Hieracium murorum</i>	FHHIEMUR
% of herbaceous <i>Laburnum alpinum</i>	FHLABALP
% of herbaceous <i>Lonicera xylosteum</i>	FHLONXYL
% of herbaceous <i>Melampyrum silvaticum</i>	FHMELSIL
% of herbaceous <i>Mercurialis perennis</i>	FHMERPER
% of herbaceous <i>Milium effusum</i>	FHMILEFF
% of herbaceous <i>Petasites albus</i>	FHPETALB
% of herbaceous <i>Picea excelsa</i>	FHPICEXC
% of herbaceous <i>Prenanthes purpurea</i>	FHPREPUR
% of herbaceous <i>Ribes alpinum</i>	FHRIBALP
% of herbaceous <i>Rubus idaeus</i>	FHRUBIDA
% of herbaceous <i>Rubus saxatilis</i>	FURUBSAX
% of herbaceous <i>Sesleria coerulea</i>	FHSESCOE
% of herbaceous <i>Sorbus aria</i>	FHSORARI
% of herbaceous <i>Sorbus aucuparia</i>	FHSORAUC
% of herbaceous <i>Vaccinium myrtillus</i>	FHVACMYR
% of herbaceous <i>Vaccinium vitis-idaeae</i>	FHVACVIT
% of herbaceous <i>Valeriana montana</i>	FHVALMON
% of herbaceous <i>Veratrum album</i>	FHVERALB

Appendix 4.

Scores values for the seven first factors (out of 37) of ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor	Specialisation factor					
	(49%)	1 (11.3%)	2 (6.7%)	3 (4.8%)	4 (4.8%)	5 (3.2%)	6 (2.3%)
FARAMEA	-0.33	-0.87	-0.12	-0.13	0.19	0.07	-0.33
FUNPMEA	-0.32	0.26	-0.29	-0.01	-0.48	-0.4	-0.19
DNORSKI	-0.31	0.09	-0.02	0.14	0.07	-0.06	0.09
FBUI	-0.23	0.1	-0.28	-0.55	-0.21	0.56	0.32
FROA	-0.19	0.01	-0.02	-0.02	0	0.05	0.06
DALPSKI	-0.19	0.02	-0.35	0.12	0.36	0.02	0.05
FTHICK	-0.19	0.01	-0.03	0.01	-0.04	0.08	-0.03
DSLEDOG	-0.13	0	-0.2	0.12	0.07	0.01	0.19
FSAMFOR	-0.11	-0.01	-0.05	0.02	-0.01	0	0.02
FFAR	-0.11	-0.04	0.19	0.68	-0.55	0.19	-0.04
FROABOR	-0.08	0	0.15	0.18	0.04	0.03	0.22
FMARSH	-0.06	-0.06	0.1	0.05	-0.21	-0.62	0.39
FWOOARE	-0.06	0	0.01	0.01	0.03	0	0.03
EXPSIN	-0.04	0.01	-0.01	0	0.01	-0.01	0.02
FAFFOR	-0.03	-0.03	-0.01	0	0.04	0	-0.03
SLOPE	-0.02	0.04	0	-0.02	0.04	-0.06	-0.02
DROA5	-0.02	0	0	0	0.01	0.04	0.01
FSHRLAN	-0.01	0.01	0.04	0.01	-0.03	-0.01	-0.01
FBUSALP	-0.01	0.01	-0.02	0.01	0.01	-0.02	0.02
EXPCOS	0.02	-0.01	-0.01	0	-0.03	0.02	-0.01
WILDBOA	0.03	-0.01	0.11	-0.07	0.09	-0.04	-0.04
FROCK	0.03	0	-0.03	0.02	-0.02	0	-0.02
FSMAFOR	0.04	0.07	-0.07	0.1	0.08	-0.07	-0.42
DROA6	0.04	-0.03	-0.03	-0.01	-0.03	0.02	0.02
DALLROA	0.06	0	0.01	0.01	0	-0.02	-0.01
DROA3	0.08	0	0.01	0	0.03	0	0.01
FROCKALP	0.1	0.01	0	0.02	0	-0.01	-0.02
FUNPGRA	0.1	0	0	-0.01	-0.01	-0.01	0
FALP	0.1	-0.03	-0.17	0.12	-0.02	-0.15	-0.08
FDEVFOR	0.11	0	0	0	0.08	-0.02	-0.01
DROA4	0.13	0	0.01	-0.01	0	0.06	0
FISOTREE	0.16	-0.06	0.05	-0.07	0	0.16	0.47
DSNOSHO	0.18	0.06	-0.07	-0.02	0.11	-0.04	-0.03
FFOR	0.18	-0.03	-0.28	0.25	0	-0.04	-0.14
DROA1	0.26	-0.05	0.05	0.07	-0.03	0.14	0.22
FOPEFOR	0.31	0	0.01	0.03	0.03	0.01	-0.02
ELEV	0.38	-0.36	-0.63	-0.2	-0.39	-0.04	-0.14

Appendix 5.

Scores values for the two first factors (out of 56) of ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor (41.2%)	Specialisation factor 1 (51%)
FCANCOV	-0.22	0.01
FCFAGSIL	-0.19	0
FHLONXYL	-0.16	0.01
FHMERPER	-0.15	0.01
FHFAGSIL	-0.12	0
FHELYEUR	-0.11	0
FUFAGSIL	-0.11	0
FUND	-0.07	0
FHABIALB	-0.06	0
FUROSCAN	-0.05	0
FHMILEFF	-0.04	0
FHFESALT	-0.04	0
FUABIALB	-0.04	0
FCSORARI	-0.04	0
FHSORARI	-0.03	0
FHRIBALP	-0.02	0
FHSESCOE	-0.02	0
FURIBALP	-0.01	0
FUNC	0	0
FHRUBIDA	0	0
FHDESCES	0.01	0
FHLABALP	0.02	-0.75
FUSORARI	0.02	0
FURUBIDA	0.03	0
FULABALP	0.03	0.66
FHHIEMUR	0.04	0
FHCARPEN	0.05	0
FHACEPSE	0.05	0
FCSORAUC	0.06	0
FHVERALB	0.06	0
FHEPIANG	0.06	0
FCACEPSE	0.07	0
FCABIALB	0.07	0
FHPICEXC	0.09	0
FHCALVAR	0.1	0
FUACEPSE	0.1	0
FHDRYFIL	0.11	0
FHPREPUR	0.12	0
FHATHFIL	0.12	0
FHRUBSAX	0.14	0
FULONNIG	0.14	0
FUPICEXC	0.14	0
FHCARDEF	0.16	0
FHSORAUC	0.17	0
FCPICEXC	0.17	-0.01
FHCARHEP	0.18	0
FHER	0.18	0

FHGENLUT	0.2	0
FHVALMON	0.2	0
FUSORAUC	0.21	0
FHADEALL	0.23	0
FHPETALB	0.24	0
FHMELSYL	0.25	0
FUSORCHA	0.26	0
FHVACVIT	0.27	0
FHVACMYR	0.27	0

Appendix 6.

Scores values for the seven first factors (out of 66) of ENFA. Values in brackets indicate the amount of variance explained by factor. Positive values of marginality factor indicate that capercaillie prefers higher values for this EGV than average for study area. Signs have no importance for specialisation factor.

Parameter	Marginality factor	Specialisation factor					
	(48.4%)	1 (31.6%)	2 (2.5%)	3 (1.4%)	4 (1.3%)	5 (1.1%)	6 (0.9%)
MCANCOV	-0.2	-0.01	0.07	0.12	0.06	-0.03	-0.09
FCFAGSIL	-0.17	0.01	0.06	0.12	0.21	0.15	-0.03
WILDBOA	-0.16	-0.03	-0.25	-0.51	-0.06	0.25	0.32
FULONXYL	-0.15	0	0.02	-0.06	0.26	-0.32	-0.22
DNORSKI	-0.15	-0.03	-0.05	0.02	0.02	0.02	-0.01
FHMERPER	-0.14	-0.02	0.78	-0.4	-0.26	-0.13	0.25
FHFAGSIL	-0.11	-0.01	0.03	0.04	-0.03	-0.1	0.01
FROA	-0.1	0.03	0.11	0.24	-0.03	-0.14	-0.12
FHELYEUR	-0.1	-0.01	0.11	0.02	0.08	-0.04	-0.08
FUFAGSIL	-0.1	0.02	0.05	-0.1	-0.03	0.12	0.11
FFAR	-0.09	0.96	-0.17	-0.22	-0.06	-0.01	0.06
FUND	-0.07	0	-0.07	-0.04	-0.01	-0.11	-0.04
FCABIALB	-0.06	-0.01	0.02	-0.04	0.03	0.09	-0.01
FFAR	-0.05	-0.14	0.1	0.42	0.02	-0.27	0.62
FHABIALB	-0.05	0.01	0.04	0.03	-0.01	-0.12	-0.07
SLOPE	-0.05	-0.01	-0.02	-0.04	0.06	0.16	0.09
EXPSIN	-0.04	0	0	0.05	-0.05	-0.09	-0.01
FCSORARI	-0.04	-0.01	-0.03	0	-0.08	0.17	0.1
FUABIALB	-0.04	0.01	-0.02	0.03	-0.01	0.02	-0.03
FUROSCAN	-0.04	0	0.1	0.3	-0.75	0.25	-0.17
FHMLEFF	-0.03	0	0.02	-0.03	-0.02	0.02	0.12
FHFESALT	-0.03	0.01	0.05	-0.05	0.05	0.03	-0.1
FHSESCO	-0.02	0	-0.03	0.03	-0.01	0.15	0.02
FURIBALP	-0.01	0	0.03	0.04	-0.01	0.01	-0.1
DSLEDOG	0	-0.01	-0.08	0.17	-0.09	-0.22	-0.07
FUNC	0	0.01	-0.08	-0.08	-0.02	-0.21	-0.08
FURUBIDA	0	0	0.04	-0.01	-0.06	0	-0.17
FHDESCES	0.01	0	-0.02	-0.01	-0.04	0.06	-0.02
FUSORARI	0.02	0	0	-0.02	-0.03	-0.06	-0.03
EXPCOS	0.02	0	0.02	0.01	-0.05	-0.09	-0.05
FURUBIDA	0.03	-0.01	-0.03	-0.04	0.04	-0.02	0.04
FULABALP	0.03	0	-0.03	0.01	0.01	0.08	0.05
DALPSKI	0.03	0.02	-0.1	-0.08	-0.27	-0.73	0.04
FHHIEMUR	0.03	0	-0.03	-0.05	-0.03	-0.01	0.02
FUCARPEN	0.04	0	-0.05	0.01	-0.04	0	-0.03
FHACEPSE	0.04	0	-0.08	0.04	-0.06	0.09	0.1
FCSORAUC	0.05	0	-0.04	-0.04	0.01	0.07	0.03
FHVERALB	0.05	0	-0.04	-0.01	0.03	0.02	0.02
FHEPIANG	0.06	0	-0.03	-0.06	0.07	0.03	0.03
FCACEPSE	0.06	0	-0.01	0	0.07	0.03	0.01
FUPICEXC	0.08	0.03	0.01	0.07	0.13	-0.03	-0.05
FUCALVAR	0.09	0.01	0.01	0.01	-0.02	0.03	-0.03
FUACEPSE	0.09	-0.01	0.05	0.01	0.01	-0.12	-0.09
DALLROA	0.09	0	-0.05	0.01	-0.01	-0.01	0.01
FHDRYFIL	0.1	0	-0.02	0.05	-0.06	-0.09	-0.05
FHPREPUR	0.11	0.01	-0.03	-0.03	-0.05	0.06	-0.04
FHATHFIL	0.11	0.01	0	0.01	0.03	0.05	0.1
DSNOSHO	0.11	-0.01	0.03	-0.24	0.04	-0.17	-0.06
FURUBSAX	0.12	0	0	0.06	-0.03	0.05	0
FULONNIG	0.13	-0.01	0.04	-0.04	0.06	-0.05	0.05

FUPICEXC	0.13	0.01	0.1	-0.01	0.04	-0.06	0.18
FHCARDEF	0.14	0	0.01	-0.05	-0.02	0.01	0.02
FHSORAUC	0.15	0.02	0.03	-0.01	-0.03	-0.01	-0.15
FCPICEXC	0.15	0.02	0.08	0.05	0.12	0.15	0.12
FHCARHEP	0.16	-0.02	-0.04	-0.03	0	0.01	0.01
FHER	0.16	0.01	-0.08	-0.07	0.03	-0.15	-0.08
FHGENLUT	0.18	0	0	-0.02	0.01	-0.01	0.02
FHVALMON	0.19	0	0	0.06	0.02	0.06	0.09
FUSORAUC	0.19	-0.01	0.01	-0.02	-0.02	0.03	0.08
FHADEALL	0.21	-0.01	0.04	-0.04	-0.01	0.01	-0.01
FHPETALB	0.22	0	-0.02	-0.01	-0.07	-0.03	0.02
FHMELSYL	0.22	-0.01	0.05	-0.06	0.06	0.03	0.09
FUSORCHA	0.24	0	0.01	-0.03	0.01	-0.01	-0.04
FHVACVIT	0.24	0	-0.01	-0.04	-0.05	-0.05	-0.04
FHVACMYR	0.24	-0.01	-0.06	0.02	-0.2	0.2	0.2
ELEV	0.29	0.23	0.38	0.02	0.14	-0.1	-0.17
