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Limiting factors in capercaillie (*Tetrao urogallus*) conservation

Tjäderförvaltningens begränsande faktorer

Ferdinand Von Wright "Capercaillies Courting" 1864 in Ateneum Art museum, Helsinki

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Christer Moreira Boman & Andreas Pettersson

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Författare/Author	Andreas Pettersson, Christer Moreira Boman
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Handledare/Supervisor	*John P. Ball ,Institutionen för vilt, fisk och miljö/ Department of Wildlife, Fish, and Environmental Studies*
Examinator/Examiner	Tommy Mörling Institutionen för skogens ekologi och skötsel/ Department of Forest Ecology and Management
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ABSTRACT

With current extinction rates comparable with the rates of previous mass extinctions and humanities necessity of biodiversity, conservation of habitat and species should be regarded as paramount whenever planning land use.
In this paper we have focused on the Western capercaillie *(Tetrao urogallus)* an umbrella species in Eurasian boreal and temperate forests. Capercaillie numbers have been reduced in mainland Europe and British Isles during the last century mainly due to increased predator populations, habitat loss, fragmentation and degradation as a result of human development of agriculture and land use change. Human recreation in sites with capercaillie show increased levels of stress in the capercaillies which might contribute to their decline.
Programs in Scotland, Germany, Spain and Poland have the aim to aid or reintroduce populations in the capercaillies historic range. Practices with the aims to reintroduce or re-stock populations often consist of releasing individuals reared in facilities or breeding centers into suitable habitat. High mortality shortly after releasing due to high predation as a result of mal adapted physical and behavior traits leads to failure in most programs.
Predator management and new techniques that improve the physical and behavioral quality in reared capercaillies such as choice of rearing method, large flight pens, elevated roost and anti-predatory training have shown increased fitness and increased survival.
The use of PVA tools is effective when comparing different procedures or scenarios and should be used as a decision basis.

SAMMANFATTNING

Nutidens utrotningstakt som kan jämföras med takterna under de tidigare massutdöendena och mänsklighetens behov av ekosystemtjänster som upprätthålls tack vare biodiversitet bör bevarande av habitat och arter ha en tydlig roll vid planering av markanvändning.

I detta arbete har vi fokuserat på Tjäder *(Tetrao urogallus)* som anses vara en paraplyart i eurasiska boreala och tempererade skogar. På den europeiska kontinenten har tjäderpopulationer minskat det senaste århundradet främst på grund av ökat predationstryck samt degradering, fragmentering och förlust av habitat. Även mänsklig störning knuten till rekreation ger ökade stressnivåer hos tjädrar vilket kan vara en bidragande faktor till minskande populationer. I Skottland, Tyskland, Spanien och Polen finns program med mål att återintroducera eller bevara tjäderpopulationer. Liknande program präglas av låga framgångssiffror. Hög predation bland tjädrar kort efter utsläpp till viss del som effekt av underutvecklade fysiska- och psykiska egenskaper. Predatorkontroll samt nya metoder att föda upp tjädrar bidrar till ökad framgång i försök. PVA är ett verktyg som effektivt kan användas för att bedöma vilket scenario i människans försök att bevara tjäder som är mest slagkraftigt.

INTRODUCTION

For the last 250 years since the beginning of the industrial revolution, anthropogenic extinction of species has increased tremendously and in many areas of the world, the native flora and fauna has suffered extinction or reduced abundance under the weight of human exploitation (Barnosky et al., 2011). The extinction of certain species called "keystone species" is likely to cause cascading effects throughout the ecosystem which will most likely affect human livelihood (Karp et al., 2013) in the area for centuries to come (Doughty et al., 2013). Large bodies, large home ranges and slow reproduction are some factors that can put a species in the risk group for extinction (Davidson et al., 2009).

To manage large-scale conservation problems, conservationists often focus on keystone species in hopes that once the species is reintroduced or once balance is restored trough management, the population will assume its keystone role and thus improve the landscape for various species. For a species to be considered a Keystone it must have a large impact on its community or ecosystem and a disproportionately large impact in relation to its abundance (Power et al., 1996). Note that the term "umbrella species" is also commonly used in conservation management, but an umbrella species is a species that, through its specific spatial and habitat needs, paves the way for numerous other species that require less space (Simberloff, 1998).

Today there are several projects aiming to bring back keystone or umbrella species into their old native range (Merta et al., 2015, Helmstedt and Possingham, 2017, White et al., 2012); some, with the hope that structures of the old biotope will return, others with the set goal of reintroducing a locally extinct species because of the value of its presence in the area (Simberloff, 1998). Some projects fail, others succeed to varying degrees. The success of the program is important not only so that various ecosystem services are secured for the future (Gessner et al., 2010, Myers et al., 2013, Young et al., 2010). Since many of these projects are funded through donations or by public resources, it is important that they are conducted in the best possible way, both from an economic and quality aspect, so that the project has the highest possible chance of success. An example of this is the reintroduction of grey wolf (*Canis lupus*) in Yellowstone National Park (Ripple et al., 2014, White et al., 2012, Beschta and Ripple, 2012, Miller et al., 2012). Whether or not the reintroduction of a species also means a reinstatement of its former role as a keystone species is not always certain because the nature of the role and the density of the keystone population are important factors and a lag between reintroduction and effect is to be expected (Lindtner et al., 2019).

Reintroduction of species in general and of Galliformes (the family of chicken-like birds which includes grouse) in particular, is a subject with a great deal of published literature. One review paper is Effectiveness of capercaillie (*Tetrao urogallus*) reintroduction projects in Europe by D. Merta *et al*. published in 2015: overall, the results reviewed there show low success, largely due to high mortality of the released birds.

Capercaillie, the biggest species in the grouse family, most often inhabit late successional stage coniferous forests (Wegge and Rolstad, 2011) which are quite limited across Europe today. Because of the capercaillies' spatial and habitat needs, it is often considered as an umbrella species since a diversity of other species thrive in the habitat where capercaillies are found (Bollmann et al., 2004, Pakkala et al., 2003, Suter et al., 2002).

A number of capercaillie populations in Europe are in decline and great efforts are being made to conserve and increase capercaillie numbers (Merta et al., 2015). The current strategy of conservation seems generally to locate areas of high significance, often lekking areas, in order to protect these areas from various forms of habitat degradation, most commonly being forestry procedures such as final felling and thinning (Pakkala et al., 2003). In these protected areas the population might be monitored and if necessary, supported by release of individuals from other stable populations or artificially reared birds (Merta et al., 2015).

Knowledge about the impact of predators on capercaillie populations is quite high (Wegge and Kastdalen, 2007, Wegge and Rolstad, 2011, Merta et al., 2015, Merta et al., 2016, Baines et al., 2016, Brittas et al., 1992, Chesness et al., 1968, Fernandez-Olalla et al., 2012, Helldin et al., 2006, Lyly et al., 2016, Oja et al., 2018), still, one might ask if efforts to mitigate predation pressure has really been implemented at a significant level.

Goal/Hypothesis

We will explore the various factors that affect successful results when reintroducing capercaillie into its historical range in order to identify what is necessary for successful conservation.
We expect that the essential needs of the species in question has to be fulfilled in order to ensure that they may survive and procreate. Initial rapid population growth is desirable to avoid that disturbances affect the entire population and thus jeopardizing success. Even more specifically, interspecific competition and predation might be limiting factors for initial rapid growth and might therefore need to be mitigated through focused wildlife management.

MATERIAL AND METHOD

We primarily searched the Web of Science database for published literature to use in this literature review. Google scholar was also used to check so that no crucial published papers were missed because Google tends to be superior in finding work not published in the traditional refereed scientific literature like reports, evaluations, government documents and more of the so-called gray literature (i.e. non-refereed publications).

When searching the Web of Science we used the search string "((capercaillie OR (Tetrao urogallus)) AND (reintroduc* or re-establis*))" also the terms "((capercaillie OR (Tetrao urogallus)) AND (reintroduc* OR re-establis* OR predat* OR CONNECT*))" and "(((capercaillie OR (Tetrao urogallus)) AND (reintroduc* OR re-establis* OR predat* OR CONNECT* or human)))" to narrow down the volume of literature and to include a connectivity and human dimensions aspect.

Thus, the studies that were found concerned the subjects of re-introductions in general, re-introduction of Galliformes and capercaillie, galliform ecology, capercaillie ecology, habitat connectivity, conservation ecology, keystone species and peripheral populations of capercaillie. We were not interested in studies about introducing species outside of their historical range or replacing one species with another with a similar niche.
Each of the studies selected in the first round had cited literature that was interesting for this review, also citations were reviewed to get an understanding of what had happened in the scientific field since the study was published.

RESULTS AND DISCUSSION

The decline of capercaillie populations and its inability to recover despite efforts to reintroduce the species across Europe is often a result of various factors (Merta et al., 2015). The most commonly-proposed factors that likely affect the capercaillie negatively can be categorized into 3 major factors: habitat, predation and isolation (Merta et al., 2015) (Storch, 2007) (Wegge and Rolstad, 2011). Controlling the influence of these limiting factors is paramount in all reintroductions so that the reintroduced species does not suffer the same fate as the previous inhabitants.
In this section we will present the major limiting factors and how they act upon the populations, also we will discuss what intensifies and mitigates their effects.

Habitat and isolation

Habitat degradation, fragmentation and loss are associated with population decline in capercaillies and black grouse (*Tetrao terix*) (Immitzer et al., 2014), (Thiel et al., 2007), (Braunisch and Suchant, 2007). Forestry practices in the boreal forest where old growth stands are cut down and replaced with plantations however does not always have a significant effect on the capercaillie, though thinned stands had the effect of being an ecological trap (Wegge and Rolstad, 2011). Nevertheless, clear-cut practices opens the canopy which reduces bilberry *(Vaccinium myrtillus)* coverage, an important resource, because of its connection to Lepidopteran larvae. This larvae is an important source of protein for capercaillie chicks during their early stages of life (Wegge and Rolstad, 2011).

Efforts to model habitat potential for the capercaillie have been done (Braunisch and Suchant, 2007, Brzeziecki et al., 2012) and results from these studies show that bilberry occurrence, structural richness and large areas of late stage successional coniferous forests are important factors in habitat quality (Braunisch and Suchant, 2007)and references therein). Habitat fragmentation and large populations of ungulates showed increased densities of mesopredators (Baines et al., 2016, Fernandez-Olalla et al., 2012).

The capercaillie is quite easily genetically isolated due to a relatively small natal range of 2-3 km (Klinga et al., 2017) which means that they are born within 2-3 km from where they breed. Habitat connectivity is crucial so that the well-known negative effects of small isolated populations such as inbreeding depression, genetic drift and stochastic birth and death events (demographic stochasticity) does not result in local extinctions.

The spatial need of habitat for a viable capercaillie population is not certain. Two factors contribute to this uncertainty. Firstly, the sensitivity in minimum viable population analysis models (MVPA) where minor changes in model parameters such as female survival and chick survival has a great impact on what is considered a viable population size (Grimm and Storch, 2000). Secondly, capercaillie density varies greatly from 20 individuals per km^2 to only 2 per km^2 within its native range (Grimm and Storch, 2000). However, we found that 25 000 ha is considered to be the minimum area of habitat to sustain a population of 500 individuals, which has been used as a suggested rule of thumb within conservation management for capercaillie (Grimm and Storch, 2000, Merta et al., 2015).

Predation

Predation pressure from mammalian mesopredators such as red fox (*Vulpes vulpes*), pine marten (*Martes martes*) or other species of raptors like the goshawk (*Accipiter gentilis*) is the predominant cause of mortality to capercaillie populations throughout Western Europe (Wegge and Kastdalen, 2007, Wegge and Rolstad, 2011, Merta et al., 2015). During the first three weeks of a capercaillie broods' life, the mortality rate of chicks can be as great as 57 %. Up to 90 % of that mortality is due to predation (Wegge and Kastdalen, 2007). In (Merta et al., 2015) it is stated that between the years 1980 to 2000 a total of 29 reintroduction projects were conducted in six countries in western Europe. None of these projects resulted in the reconstruction of a viable population. According to (Merta et al., 2015), the greatest obstacle, and thereby the most important barrier to capercaillie reintroduction projects in Europe is the high mortality rate of birds shortly after release, predominantly caused by predation.

Another example from the (Merta et al., 2015) study is taken from a release project in the Harz mountains in the average survival rate of 83 capercaillie was 13 days. Just like in the (Wegge and Kastdalen, 2007) study, a majority of the mortality was caused by predation within the first month. Also similar to the (Wegge and Kastdalen, 2007) study and other studies concerning both capercaillie and other Galliformes (Baines et al., 2016, Brittas et al., 1992, Chesness et al., 1968, Fernandez-Olalla et al., 2012) the authors conclude that predation stood for a similar proportion of the total mortality with figures up to 79 %. In relocations, non-wild capercaillie broods show a higher susceptibility to predation than wild capercaillie.

Management for conservation

Management for conservation practices generally include habitat management, predator control, and population augmentation in varying degrees and fashion (Arroyo and Beja, 2002). Areas with capercaillie presence in continental Europe, often mountainous spruce-dominated coniferous forests and especially lek sites are protected from agriculture or forestry practices that degrade or remove suitable habitat (Oja et al., 2018).

Protection of lek sites is logically sound, being areas where the capercaillie aggregate but also since males have a rather strict requirement for old forest (Oja et al., 2018) that is suitable habitat for rearing chicks (Braunisch and Suchant, 2007, Brzeziecki et al., 2012). However, focusing only on lek sites may not be optimal due to increased predation of nests and chicks as a result of high density of prey and because generally hunting regulations within these protected areas creates a "safe haven" for foxes (Oja et al., 2018).

Success rates of the reintroduction programs for capercaillie are low in Europe. Between 1980 and 2000 29 programs were initiated in 6 countries in western Europe but not one was successful (Merta et al., 2015). A great hurdle in reintroduction of a prey species is predation (Baines et al., 2016, Lyly et al., 2016, Madden et al., 2018, Merta et al., 2015, Moreno-Opo et al., 2015, Wegge and Kastdalen, 2007). For the reintroduction of capercaillie; mortality shortly after release of captive reared chicks or of wild chicks where a vast majority were predated (Moreno-Opo et al., 2015). To reduce the effects of predation one might consider predator control or population augmentation in form of bird release. While both have positive effects on their own, with predator reduction being the most effectful option if only one strategy was practical, together they were optimal (Fernandez-Olalla et al., 2012). Population augmentation in form of bird release with the aim to restock or re-introduce for non-hunting purposes can be divided into three factors regarding the released individuals, the factors being quality, spatiality and timing. Each of these factors have a significant role in increasing survival of individuals. Which is the most important is not clear and depends on the habitat where the birds are released so variation from case to case is likely to be expected.

The quality of released birds reflects the genetic origin and the method of rearing.
Rearing methods range from artificial to semi-natural and natural. The use of egg incubators and brooders where the chicks have no contact with adult birds is considered as artificial rearing (Sokos et al., 2008). To consider a rearing as natural the eggs have to be cared for by their biological parents (Buner and Schaub, 2008, Scott and Carpenter, 1987). Semi natural rearing is a combination of natural and artificial rearing methods. In semi natural rearing the eggs lay in an incubator but are in contact with and raised by foster parents (Sokos et al., 2008). To distinguish rearing method in this way might seem unrefined. There is great variation within each method where some utilize a domestic hen (*Gallus domesticus)* (Brittas et al., 1992*)* and sometimes eggs are exposed to recorded adult vocalization during incubation (Slaugh et al., 1992). The classification is however refined enough so that we may get an understanding, discuss and see trends between each method.

The choice of rearing method depends on the aim of release, but it is also an economic question. Semi natural and natural rearing is mostly used in reintroduction and restocking programs (Carpenter et al., 1991, Schroth, 1991). Key behavior to avoid predation and to ease foraging in the wild are important to increase fitness of the released birds.
Elevated perches increased the probability that released birds found a roosting place in trees, which reduced predation during night time but also resulted in more muscle mass in the pectoral muscle (Madden et al., 2018). Differences in the size of the heart and pectoral muscles along with the size and chemical composition of the liver, are the attributes deemed connected to overall survivability and fitness (Liukkonen-Anttila et al., 2000)

Varied feed and pens with "natural" vegetation might reduce the frequency of short digestive tracts often seen in artificially reared individuals and teaching foraging behavior (Liukkonen-Anttila et al., 2000). Predation on young Galliformes is high, and even higher on captive reared Galliformes (Buechner, 1950) a proposed cause of this is the lack of contact with predators which teaches anti predatory behavior (Burger, 1964, Parish and Sotherton, 2007). The use of predatory training in brooders is limited but seem to be successful (Slaugh et al., 1992) whether it has a significant difference is however still unclear.

The release of reared capercaillies of lower quality may have a negative effect on the wild population (Leif, 1994, Putaala and Hissa, 1998, Black, 1991, Gortázar et al., 2006) the negative effects may be caused by 1) reducing survivability in offspring for the wild individuals that mates with the reared one (Rands and Hayward, 1987), 2) attracting predators and increasing predatory focus on capercaillie (Kenward et al., 1981, Hill and Robertson, 1988, Mueller, 1971) , 3) increased dieses and parasites and lastly (Millán et al., 2004, Villanúa et al., 2008), 4) genetic dilution and degradation (Barilani et al., 2007, Ford, 2002, Meriggi et al., 2002, Puigcerver et al., 2007)

Translocation of wild birds from stable populations has been proposed as the best way to successful reintroductions (Sokos et al., 2008). In Pennsylvania the release of 3000 captive reared pheasants failed to create a stable population but 1000 relocated wild birds succeeded (E. Myers, 2019)
Relocation of wild birds is expensive initially, but given that wild relocated Galliformes and their offspring have up to 23 times greater reproduction compared to artificially-reared hens

(Sokos et al., 2008) it may be more economic and effective in a long term perspective. An alternative to wild relocated birds is semi naturally reared birds that have been reared in large flight pens with natural vegetation with varied feed scattered throughout and minimal human interaction and some form of anti-predatory behavior training (Hess et al., 2005, Liukkonen-Anttila et al., 2000, Pyörnilä et al., 1998).

The effect of mesopredator removal seems to be most significant for increasing survival of chicks, with little effect is seen on adults (Moreno-Opo et al., 2015), which we expected. However, areas where lower populations of adult birds seem to corelate with high fox populations (Baines et al., 2016). For predator control to have a significant effect, it has to be performed over large spatial scales, such as 41km^2 (Chesness et al., 1968, Frey et al., 2003) One might consider the capercaillie population being in a so called "predator pit", which is the theory that there are more than one points of equilibrium between prey populations and predator populations. This could motivate a severe removal of mesopredators during a short time span during which the capercaillie population is established and once strong, the predators are no longer a major threat for the existence of the capercaillie population; the system is not at a different equilibrium point.

We do however agree with (Fernandez-Olalla et al., 2012) that population augmentation and predator control is a form of crisis management. For success in the long run, managers must move away from time and resource-consuming interventions that are common today and rather focus on attempting to restore the ecosystem to what it once was. However, with the fragmented landscapes of today that favor mammalian mesopredators and corvids (Baines et al., 2016), extensive predator control may be the most effective method that can be implemented in the short term to preserve capercaillie reintroductions. In addition to predator hunting or other types of focused management strategies, there are ways to balance predation by mesopredators through recovery of apex predators (Moreno-Opo et al., 2015). A suitable apex predator to reintroduce in various parts of Europe is the Eurasian lynx (*Lynx lynx).* The effects of lynx on mesopredators and capercaillie has been studied in Sweden where they found that increased lynx numbers decreased fox abundance and in turn increased the capercaillie and black grouse population (Helldin et al., 2006, Moreno-Opo et al., 2015).

Another aspect to consider with capercaillie management is the effect of human disturbance which is seen by some as a serious conservation issue for many threatened species (Thiel et al., 2007). Winter recreational areas like ski resorts in the alpine regions of Europe are often sites where capercaillies are still found in Europe (Thiel et al., 2011). Capercaillies have shown increased stress levels in areas where human recreational activity is higher (Storch, 2013, Thiel et al., 2008, Thiel et al., 2007, Coppes et al., 2018, Thiel et al., 2011), and surprisingly only in forests dominated by Norway spruce (*Picea abies) (Thiel et al., 2011).* Increased stress levels may have direct negative effects on an individual's immune system and contribute to capercaillie decline (Thiel et al., 2011, Madden et al., 2018). To avoid and diminish anthropogenic disturbance, managers could enter requirements that skiers and hikers must remain on the trails where inter-trail distance is less than 100m, since most cases of flushing capercaillie happened within 50m of the bird (Thiel et al., 2007) and creating buffer zones 50m around the trails to avoid flushing and thus disturbing birds (Immitzer et al., 2014). Possibly some sites should be left totally without human disturbance during parts of the year when disturbance can have large effects on productivity, such as the lek and rearing periods.

Thoughts and conclusions about the future of capercaillie management

We ask ourselves what point there is in investing money and focusing on an umbrella species such as the capercaillie that is not viable without intensive interventions. The motivations for capercaillie conservation are often that its presence signals a certain habitat with its unique flora and fauna. If this umbrella species is not viable and as our review shows that this lack of viability is largely due to low habitat quality, should not resources and future research be allocated to habitat restoration?

In order to ensure that we maximize the benefit of our limited resources of today, our management decisions need to be right for our needs tomorrow. Limiting factors such as time, space and money put us in situations where we are unable to do everything. We need to weigh our alternatives and prioritize our efforts so that our future allocation of resources isn't wasted. One way to do this is to use the proper tools to support our decision-making. One of the best tools we have as of today is population viability analysis.

Population viability analysis or PVA for short is a very useful tool for strategic conservation and with that in mind we will end this paper by presenting this tool. PVA is a process to analyze data and create a model which can give the user information about the future of a given population (L. Shaffer, 1981, Shaffer, 1987). The foundation for the models is that extinction is a series of stochastic elements (L. Shaffer, 1981, SHAFFER, 1980) which are separated into demographic and environmental stochasticity (May, 1973). Demographic stochasticity refers to events that happens within the population, such as the two last surviving individuals of a species both being of the same gender. Environmental stochasticity refers to changes in habitat, climate etc.

There is a third component that (L. Shaffer, 1981) distinguished which is genetic stochasticity where founder effect, inbreeding and genetic drift are responsible for changes in allele frequency (Thompson, 1991). There are three categories of PVA suggested by Thompson:

1. Simulation of different scenarios to evaluate which is better suited for the purpose, this is the most commonly used method of PVA
2. "rules of thumb" such as minimum viable population of a given species.
3. Analytical methods such as birth and death models.

Today PVA is often used when describing the method of analyzing a population and reviewing the different management scenarios which estimates the probability of a species surviving into a given time in the future. The use of PVA has been critiqued for its lack of standardization, low reliability in risk classification and inconsistency in methods and varying assumptions (Lindenmayer et al., 1995, Taylor, 1995). Important processes which need data such as density dependence and spatial structure are hard to understand and estimate since there is not always a lot of data on endangered species. As long as the uncertainty of PVA is embraced it can still be a valuable tool to compare and prioritize management actions now and in the future. PVA might not be able to accurately tell us if capercaillie will be around in the Cantabria in 70 years but it can shed light on dynamic relationships that affect the capercaillie, find data gaps and (most importantly) compare different management scenarios (Boyce, 1992). For a truly effective and successful conservation of capercaillie, we suggest that PVA tools should be more widely used to make decisions.

Through our review of the literature published about the capercaillie and its reintroductions, we’ve seen that the populations in continental Europe are diminishing as a result of habitat loss, degradation and fragmentation. What characterizes capercaillie habitat was not old growth forest with some form of wetland fragmentation as we initially thought. Ericaceae shrubs and primarily bilberry shrubs together with low proportions of farmland create potential habitat. Existing trials to reintroduce the species both today and in the past fail. Mostly because of high mortality rates due to predation as we initially thought, and the maladaptation of artificially-reared individuals. In order to mitigate these effects and to achieve functioning and healthy populations we conclude that in short term, we should engage in strong predator control for a limited time, and transition from releasing-artificially reared birds to wild-caught birds for translocation. PVA tools should be used so that managers and decision makers can compare different procedures or scenarios and make the best choices for long term management. Finally, more research in what makes predator control, capercaillie rearing and habitat improvement more efficient and effective is needed.

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