Survival, habitat use and disturbance behaviour of re-introduced Grey Partridges *Perdix perdix* L. in an enhanced arable landscape in the Swiss Klettgau

Inauguraldissertation

zur

Erlangung der Würde eines Doktors der Philosophie

vorgelegt der

Philosophisch-Naturwissenschaftlichen Fakultät

der Universität Basel

von

FRANCIS D. BUNER

aus Basel

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Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät auf Antrag der Herren Professoren Dr. B. Bruderer und Dr. B. Baur.

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Wenn man sich die Gefahren vergegenwärtigt, denen das Rebhuhn ausgesetzt ist, bevor es sein volles Wachstum erreicht hat – alle vierfüssigen Räuber, Edelfalk, Habicht, Sperber, Bussard, Weih, Raben und Häher, egal ob jung oder alt, sind fortwährend auf seinen Fersen - und bedenkt, dass es der bösen Witterung noch ausserdem Stand halten muss, begreift man kaum, wie es möglich ist, dass es überhaupt noch Feldhühner gibt.

Alfred Brehm 1861

If one visualises the threats to which a Grey Partridge is exposed before it has reached its adult size – including all predators on four paws, peregrine falcons, goshawks, sparrow hawks, buzzards, harriers, crows and jays either young or adult and never off its back – and if one further considers that it has to cope with our bad weather, then it is hard to comprehend why partridges are actually still around.

translation, F. Buner

SUMMARY

Background

In the last forty years, the Swiss lowlands have lost much of their former value as habitat for wild plants and animals, mainly because of the effects of modern farming practices. One of the most prominent and charismatic species affected is the Grey Partridge *Perdix perdix L.* Considering the alarming decline of the Grey Partridge, the Swiss Agency for the Environment, Forests and Landscape (SAEFL) entrusted the Swiss Ornithological Institute in 1991 to undertake a ten year project on "Protection measures for brown hare and Grey Partridge" (Jenny *et al.* 2002). In this context the "Klettgau" in the canton of Schaffhausen was chosen as study area as it was one of the two regions in Switzerland where wild partridges still remained in small numbers at that time. To reverse the main cause of the partridge's decline - habitat loss - the main activity in the early stages of the project was the promotion of ecologically enhanced habitats such as wild-flower strips and hedges. Unfortunately, the already very small partridge population went extinct shortly after the beginning of the project. However, by 1998 the area of partridge-friendly habitats had grown to such an extent that it allowed to launch a partridge re-introduction project. This was undertaken as part of the Swiss Ornithological Institute's project "Birds as test organisms to evaluate enhanced habitat diversity in agricultural areas" which was launched in 1996.

The main aims of this thesis for which the data was collected between 1998 and 2001 are to assess whether Grey Partridges:

1) are able to survive and reproduce in an ecologically enhanced landscape such as the Klettgau,

2) make use of the enhanced areas and, if so, which value they have for them,

3) are disturbed by human and predator activities within the re-introduction area,

4) to conclude if and under what conditions further partridge re-introductions in Switzerland might be successful.

Study area

The study area (c. 530 ha) is intensively cultivated, mainly for growing cereals (49%), oil-seed rape and sunflowers (14%) and root crops (12%). Grassland covered 11%, another 11% were bare of vegetation (buildings, roads, etc). Permanent cover such as wild-flower strips, hedgerows and grass banks amounted to 3% of the area. Field sizes ranged from 0.1 to 5.5 ha.

From 1991 to 2001 the area of wild-flower strips increased from 0 ha to 12 ha, the area of hedgerows from 2 ha to 2.7 ha. Besides agricultural use, the study area is very popular for recreation mainly by walkers with or without dogs and riders. In the centre of the study site there is a dog training school and an arena to school horses, in the northern part of the area there is a cycling route.

Origin of birds released

Originally it was planned to release wild translocated birds of the western clade of the subspecies *Perdix perdix perdix* only (50 per year) as it is widely accepted that this technique generates the highest possible re-introduction success in areas where the species has become extinct. After the first year of this study however, it became apparent that it was impossible to organize enough wild-caught birds for release (n = 21 released in total). I therefore had to switch to the next most promising option which I considered to be parent-reared birds released as coveys in autumn (n = 77). In the second and third year of this study we additionally fostered parent-reared chicks to already re-established adult birds which had failed to produce their own young (n = 32).

Dispersal, survival and causes of death

Of the 98 released adult partridges, 73% remained within the study area and 52% survived the first month after release. During the first month after release, they frequently moved across the whole research area. After settling, 98% of all partridge locations were recorded in that part of the study area where the density of enhanced areas was maximal.

Survival was highest in wild-hatched partridges of the founder population (mean ± SE; 0.90 ± 0.03), followed by that of fostered chicks (0.86 ± 0.03) and translocated adult wild birds (0.82 ± 0.06). While survival of these groups was not statistically different from each other, survival of captive-reared adults was significantly lower (0.70 ± 0.06). We found the carcasses of 91 partridges. 88 of them were predated, 1 died because of disease, 1 because of a traffic accident and 1 as a result of a territorial fight. Predation by mammals (mainly foxes) was twice as frequent as predation by avian predators.

Reproductive success

We observed 19 pairs that started egg laying. Of those, seven broods hatched and twelve failed. Mean clutch size of first clutches was 15.6 eggs (N = 9 clutches, SD = 1.3). Only one

second clutch was found. 86% of all eggs hatched (N = 7 broods). The average percentage of successful nests over three years was only 0.33 [SE = 0.08]. When breeding the year after release, fostered chicks tended to have more successful nests (0.44 [SE = 0.43]) than when individuals of the other treatment groups were involved (reared adults: 0.17 [SE = 0.03]; translocated: 0.25 [SE = 0.07]; wild hatched in study area: 0.27 [SE = 0.29]), but the differences were not statistically significant. Eleven out of 19 nest were located in wild-flower strips.

Habitat use and home range size

At the level of the individual family group (pairs or coveys), we found a significantly greater use (throughout the year) of habitat areas that were enhanced with wild-flower strips and/or hedges, compared to non-enhanced areas. When the birds used the agricultural fields, densities of use declined sharply with increasing distance from the nearest enhanced area. Thus, the availability and spatial distribution of ecologically enhanced areas were the main determinants of the partridges' range use. Despite their strongly over-proportional use of enhanced areas, the partridges spent a large proportion of time in cultivated fields. In summer, frequently visited vegetation types were cereals (average 26.1% of locations), root crops (14.8%) and grassland (9.3%). In winter, the birds spent much of their activity in cereals or stubble fields (32.7%) and rape (24.1%). This indicates that these types of vegetation, particularly cereals, were attractive resources, although not preferred in respect to their availability.

The size of the group home-ranges varied significantly with season. In spring (pre-breeding period) and summer (breeding period), the average home-ranges (± SD) were 6.8 (± 4.0) ha and 6.9 (± 2.6) ha, respectively. From late summer until the end of winter (non-breeding period), the home-ranges were significantly larger; late summer: 15.2 (± 6.6) ha; autumn: 17.0 (± 4.0) ha; winter: 14.4 (± 3.6) ha.

Disturbance

Partridges showed a distinctive cause-specific reaction repertoire to all disturbance types compared, mainly crouching in presence of raptors and showing vigilance in presence of mammals (foxes and cats). Flushing was the main reaction when disturbed by leisure activities. When flushed, partridges reduced their flight distance by 54 metres compared to unforced flights and remained in their territory in 87% of all cases. In summer, their main

escape cover was cultivated fields, whereas in winter they mainly used permanent cover such as wild-flower strips and hedges. The spatial distribution of partridges was influenced by season: In summer, partridges avoided areas with high human disturbance, whereas in winter they avoided areas with high predator abundance and close proximity to tall hedges. Human activities caused twice as much disturbance events as predators, with associated energetic costs. Overall, disturbance substantially limited overall spatial use, with consequences for the carrying capacity of the area.

Conclusion

This study shows that with enough staying power even the intensively exploited Swiss countryside may provide a satisfactory environment for a highly demanding species such as the Grey Partridge. Even though it is not possible to prove from this study's results if further partridge re-introductions in Switzerland or abroad will be successful in terms of creating self-sustainable populations – for that the duration of the study was simply too short - it is possible to draw four basic conclusions for future partridge re-introduction projects:

1) Prior to every partridge re-introduction or re-establishment the habitat must be enhanced with permanent habitat structures such as hedgerows and wild-flower strips.

2) If translocated wild birds are not available for release, chicks should be fostered whenever possible, in the best case to wild birds still resident in the area.

3) Re-introductions should only be envisaged in areas with low predator numbers and human activities.

4) In order to find possible weaknesses in re-introduction projects, post-release monitoring is essential to ensure the project targets are met.

ZUSAMMENFASSUNG

Hintergrund

Das Schweizerische Mittelland hat in den vergangenen vierzig Jahren - insbesondere wegen den negativen Einflüssen der modernen Landwirtschaft - seinen ehemaligen Wert als Lebensraum für Pflanzen und Tiere des Agrarraumes weitgehend verloren. Eine der wohl charakteristischsten sowie charismatischsten dieser Arten ist das Rebhuhn *Perdix perdix L.* In Anbetracht des alarmierenden Bestandesrückgangs des Rebhuhns in der Schweiz, beauftragte das Eidgenössische Bundesamt für Wald und Landschaft (BUWAL) die Schweizerische Vogelwarte 1991 mit dem Projekt „Schutzmassnahmen für Feldhase und Rebhuhn", welches im Jahr 2000 abgeschlossen wurde (Jenny *et al.* 2002). In diesem Zusammenhang wurde der Schaffhausische Klettgau als Untersuchungsgebiet gewählt, da dieser zu jener Zeit nebst der Champagne genevoise die letzte Region mit wildlebenden Rebhühnern in der Schweiz war. Um die Hauptursache des Rebhuhnrückganges - der Verlust an geeignetem Lebensraum – zu beseitigen, konzentrierte die Vogelwarte ihre Anstrengungen in den ersten Jahren auf Lebensraumaufwertungen, insbesondere durch die Propagierung von Ökologischen Ausgleichsflächen wie Buntbrachen und Hecken. Unglücklicherweise starb jedoch der bereits sehr kleine Rebhuhnbestand kurz nach der Projektaufnahme aus. Bereits im Jahr 1998 hatte dank den Habitataufwertungen der Anteil an rebhuhntauglicher Nutzfläche einen Stand erreicht, welcher eine Rebhuhn-Wiederansiedlung theoretisch möglich machten. Diese Überlegungen fanden 1996 ihren Ursprung im Rahmen des im selben Jahr von der Vogelwarte Sempach initiierten Projektes „Vögel als Testorganismen zur Evaluierung ökologischer Habitataufwertungen im Agrarraum". Diese Arbeit ist Teil dieses Projektes.

Diese Dissertation, für welche die Daten zwischen 1998 und 2001 gesammelt wurden, untersucht folgende Hauptaspekte:

1) Sind ausgesetzte Rebhühner fähig in einer ökologisch aufgewerteten Agrarlandschaft wie dem Klettgau zu überleben und zu reproduzieren?

2) Nutzen ausgesetzte Rebhühner die aufgewerteten Flächen und wenn ja, welchen Wert haben diese für die Rebhühner?

3) Werden die Rebhühner im Freilassungsgebiet durch menschliche Aktivitäten und Räuber gestört und welchen Einfluss habe diese auf das Rebhuhn?

4) Unter welchen Bedingungen sind Rebhuhn-Wiederansiedlungen in der Schweiz erfolgreich?

Untersuchungsgebiet

Das Untersuchungsgebiet (ca. 530 ha) wird landwirtschaftlich intensiv genutzt, hauptsächlich für den Getreideanbau (49%), Raps und Sonnenblumen (14%) sowie Zuckerrüben (12%). Der Wiesenanteil betrug 11%, wie auch derjenige der bebauten Nutzfläche (Gebäude, Strassen, usw.). Permanente Deckungsstrukturen wie Buntbrachen, Hecken und Grasborde bedeckten 3% der Fläche. Die Feldgrössen schwankten zwischen 0.1 und 5.5 ha. Zwischen 1991 und 2000 stieg die Fläche der Buntbrachen von 0 ha auf 12 ha, diejenige der Hecken von 2 ha auf 2.7 ha. Nebst der landwirtschaftlichen Nutzung ist das Gebiet sehr populär für Freizeit-aktivitäten und Erholung, insbesondere Spaziergänger und Reiter mit und ohne Hunden nutzen das Gebiet intensiv. Im Zentrum befindet sich ausserdem eine Hundesportschule sowie ein Reitplatz und durch den nördlichen Teil führt ein Fahrradweg.

Herkunft der ausgesetzten Rebhühner

Ursprünglich war die Freilassung von jährlich 50 Wildfängen der westlichen Rasse *Perdix perdix perdix* vorgesehen, da diese – insbesondere in Gebieten wo die Art verschwunden ist - den besten Wiederansiedlungserfolg versprechen. Nach dem ersten Untersuchungsjahr zeigte sich jedoch, dass die Beschaffung einer ausreichenden Anzahl Wildfängen logistisch unmöglich war (insgesamt 33 ausgesetzt). Aus diesem Grund setzten wir zusätzlich jeweils im Herbst von Rebhühnern ausgebrütete Familienverbände aus (i.w. gezüchtete Altvögel), was ich als best mögliche Alter-native betrachtete (77 freigelassen). Im zweiten und dritten Untersuchungsjahr setzten wir zusätzlich von Rebhühnern ausgebrütete Jungvögel frei (i.w. adoptierte Jungvögel), welche wir von erfolglos brütenden, bereits re-etablierten Paaren adoptieren liessen (32 freigelassen).

Dispersion, Überleben und Todesursachen

Von den insgesamt 110 freigesetzten adulten Rebhühnern, verblieben 73% innerhalb des Untersuchungsgebietes und 52% überlebten den ersten Monat nach deren Freilassung. Während des ersten Monats nach Aussetzung waren die Hühner im gesamten Untersuch-ungsgebiet anzutreffen. Nach dieser Ansiedlungsphase befanden sich 98% der Rebhuhn-ortungen in jenem Teil des Gebiets mit der höchsten Dichte an ökologischen Ausgleichs-flächen. Die beste Überlebensrate ($\bar{x} \pm$ SE; 0.90 $\pm$ 0.03) wurde von im Untersuchungs-gebiet geschlüpften Individuen erzielt (F1 Generation von im Rahmen dieser Arbeit ausgesetzten Individuen), gefolgt von den adoptierten Jungvögeln (0.86 $\pm$ 0.03) und den

Wildfängen (0.82 ± 0.06). Während die Überlebensrate dieser drei Gruppen sich statistisch nicht signifikant voneinander unterschied, war jene der gezüchteten Hühner signifikant tiefer (0.70 ± 0.06).

Von 91 gefunden Rebhuhnüberresten waren 88 von Räubern erbeutet, 1 starb auf Grund von Krankheit, 1 durch Verkehr und 1 an Revierkampfverletzungen. Prädation durch Säuger (v.a. Füchse) war doppelt so häufig wie jene durch Greifvögel.

Bruterfolg

Von 19 beobachteten Paaren welche mit der Eiablage begannen, führten 7 zu Bruterfolg und 12 zu Brutverlust. Die durchschnittliche Gelegegrösse für Erstgelege betrug 15.6 Eier (N = 9 Gelege, SD = 1.3). Nur eine Zweitbrut wurde gefunden. Die Schlupfrate betrug 86% (N = 7 Gelege). Der durchschnittliche Anteil an erfolgreichen Bruten betrug nur 0.33 (SE = 0.08). Individuen welche im Jahr nach ihrer Freilassung brüteten, schienen einen höheren Nesterfolg zu haben (0.44 [SE = 0.43] als jene aus den anderen Freilassungsgruppen (gezüchtete Alt-vögel: 0.17 [SE = 0.03]; Wildfänge: 0.25 [SE = 0.07]; Individuen der F1 Generation: 0.27 [SE = 0.29]). Die Unterschiede waren jedoch statistisch nicht signifikant. Elf von 19 Nestern befanden sich in Buntbrachen.

Habitatnutzung und Grösse des Aktionsraums

Im Vergleich zu den nicht aufgewerteten Gebieten ergab sich für Rebhuhnpaare und Ketten (i.w. Gruppen) eine übers gesamte Jahr signifikant höhere Nutzung von Flächen welche mit Buntbrachen und/oder Hecken aufgewertet waren. Die Nutzungsdichten von Rebhuhn-Ortungen in kultivierten Feldern, sanken drastisch mit steigender Distanz zur nächsten aufge-werteten Fläche. Aus diesem Grund war die Verfügbarkeit und Verteilung von ökologisch aufgewerteten Flächen die Hauptdeterminante der Rebhuhn-Lebensraumnutzung. Trotz ihrer stark überproportionalen Nutzung von aufgewerteten Flächen, verbrachten die Rebhühner einen Grossteil ihrer Zeit in kultivierten Feldern. Regelmässig genutzte Vegetationstypen im Sommer waren Getreide ($\bar{x}$ = 26.1% der Ortungen), Zuckerrüben (14.8%) und Wiesen (9.3%). Im Winter verbrachten die Hühner einen Grossteil ihrer Aktivität in Stoppelfeldern (32.7%) und Raps (24.1%). Dies deutet darauf hin dass diese Vegetationstypen, insbesondere Getreide, eine attraktive Ressource darstellen, obwohl diese in Anbetracht ihrer Verfügbarkeit nicht bevorzugt wurden.

Die Grösse der Rebhuhngruppen-Aktionsräume variierte saisonal signifikant. Die mittlere

Aktionsraumgrösse (± SD) im Frühling (Brutrevierbegründungsphase) betrug 6.9 (± 2.6), jene im Sommer (Brutsaison) 6.8 (± 4.0) ha. Vom Spätsommer bis Ende Winter (Periode ausserhalb Brutsaison) waren die Aktionsräume signifikant grösser; Spätsommer: 15.2 (± 6.6) ha; Herbst: 17.0 (± 4.0) ha; Winter: 14.4 (± 3.6) ha.

Störung

Die Rebhühner zeigten ein klares ursachenspezifisches Reaktionsverhalten gegenüber allen untersuchten Störungstypen, hauptsächlich „Ducken" bei Anwesenheit von Greifvögeln und „Sichern" bei jener von Säugern (Katzen und Füchse). Bei durch Freizeitaktivitäten verursachten Störungen reagierten die Hühner hauptsächlich mit „Auffliegen". Aufgescheuchte Rebhühner reduzierten im Vergleich zu störungsunabhängigen Flügen ihre Flugdistanz um 54 Meter und verblieben in 87% aller Fälle innerhalb ihrer Territoriumsgrenze. Im Sommer nutzten sie hauptsächlich kultivierte Felder zur Deckung, im Winter hingegen waren es vor allem permanente Deckungsstrukturen wie Buntbrachen und Hecken. Die Raumnutzung der Rebhühner war saisonal beeinflusst: Im Sommer mieden die Hühner Gebiete mit hoher menschlicher Störung, wogegen im Winter Gebiete mit hoher Räuberdichte und hohen Hecken gemieden wurden. Menschliche Aktivitäten verursachten insgesamt doppelt so viele Störungsereignisse wie jene verursacht durch Prädatoren, einhergehend mit energetischen Kosten für die Vögel. Störung limitierte alles in allem den insgesamt für die Rebhühner nutzbaren Raum substanziell, mit entsprechenden Konsequenzen für die Tragfähigkeit im Untersuchungsgebiet.

Schlussfolgerung

Diese Arbeit zeigt, dass mit genügend grossem Einsatz selbst das intensiv genutzte schweizerische Agrargebiet einen zufriedenstellenden Lebensraum für eine so anspruchsvolle Art wie dem Rebhuhn bieten kann. Obwohl es auf Grund der in dieser Arbeit gefundenen Resultate nicht möglich ist zu beweisen, dass Rebhuhnansiedlungen in der Schweiz oder im Ausland zu selbst-erhaltenden Rebhuhnpopulationen führen können – dazu war die Dauer der Feldstudie schlicht zu kurz – ist es möglich vier grundsätzliche Schlussfolgerungen für zukünftige Rebhuhnwiederansiedlungsprojekte zu ziehen:

1) Vorgängig zu jeder Rebhuhn-Wiederansiedlung oder Bestands-Wiederherstellung muss der Lebensraum im Aussetzungsgebiet mit permanenten Strukturen wie Buntbrachen und

Hecken wiederaufgewertet werden.

2) Falls Wildfänge zur Ansiedlung nicht zur Verfügung stehen, sollten wenn immer möglich Jungvögel zur Adoption freigelassen werden. Im besten Falle dort wo noch Wildvögel vorhanden sind.

3) Rebhuhn-Wiederansiedlungen sollten nur in Gebieten in Erwägung gezogen werden, welche eine geringer Räuberdichte und einen niedrigem Anteil an menschlichen Aktivitäten aufweisen.

4) Um mögliche Schwachstellen in Wiederansiedlungs-Projekten aufzudecken und um deren Strategie wenn nötig angleichen zu können, ist ein Post-Monitoring essentiell.

GENERAL INTRODUCTION

Background

In the last forty years, the Swiss lowlands have lost much of their former value as habitat for wild plants and animals. One of the most prominent of the affected species is the Grey Partridge *Perdix perdix* L. It was once a typical farmland bird with, in the 1960s, a spring population of about 10'000 individuals, however numbers have declined sharply since (Schmid *et al.* 1998). This was the result of intensified agricultural practices such as the change of cropping patterns from mixed farming to pure arable use with a predominance of autumn crops and an accompanying increase in the use of herbicides which have largely eliminated arable weeds. These weeds were host to insects which are the preferred prey of partridge chicks in their first weeks of life (Potts 1986, Panek & Kamieniarz 2000). Removing fallow land, hedges and grass banks has further contributed to the loss of nesting sites and cover from predators (Potts 1986, Panek 2002). These drastic changes have been accelerated by increases in the number of some predatory birds, but particularly predatory mammals (Tapper 1992, Tapper *et al.* 1996). The most important predator of the partridge is the red fox *Vulpes vulpes* (Potts 1986), the numbers of which have increased in Switzerland, partly due to the eradication of rabies (Breitenmoser *et al.* 1996).

Since 1993 Swiss farmers have been encouraged by financial incentives to establish ecological compensation areas such as wild-flower strips and hedges as part of a policy to enhance biodiversity in farmland. Considering the alarming situation, the Swiss Agency for the Environment, Forests and Landscape (SAEFL) entrusted the Swiss Ornithological Institute in 1991 to carry out a ten year project on "Protection measures for brown hare and Grey Partridge". The aim of this project was to acquire practical experience of the application of ecological enhancement measures in intensively used agricultural areas, and to support various breeding bird species of open farmland alongside these two flagship species (Jenny *et al.* 2002).

In this context the "Klettgau" in the canton of Schaffhausen was chosen as a study area because it was one of the two remaining regions in Switzerland where wild partridges still existed in small numbers at the beginning of the nineties (the other region being the "Champagne genevoise" in the canton of Geneva). However, the habitat enhancements established in the Klettgau came too late for the Grey Partridge. Shortly after the beginning of the project the already very small population went extinct (Jenny *et al.* 2002). In 1996 the Swiss Ornithological Institutes started the project "Birds as test organisms to evaluate

enhanced habitat diversity in agricultural areas". This project became part of the interdisciplinary research program "Integrated Project Biodiversity" launched by the Swiss National Science Foundation. According to the project title the main aims are:

To test whether the Grey Partridge

1)   is able to survive and reproduce in an ecologically enhanced landscape such as the Klettgau, *see chapter III*.

2)   makes use of the enhanced areas and, if so, what value they have for them, *see chapter IV*.

3)   is severely disturbed by human and predator activities within re-introduction areas, *see chapter V*.

4)   to conclude if and under what conditions further partridge re-introductions in Switzerland might be successful, *see chapter VI*.

Ecology of the Grey Partridge *(Perdix perdix)*

The Grey Partridge is a Eurasian species preferring grass steppe or open habitat of low-intensity mixed farmland with small fields, hedges and grassy banks which provide nesting cover (Potts 1986, Birkan & Jakob 1988). It is divided in seven subspecies, of which *Perdix perdix perdix* belongs to the British Islands, southern Norway and Middle Europe north of the Alps from France to the Czech Republic and Poland (Liukkonen-Anttila *et al.* 2002). This is the subspecies that was introduced to North America and is now numerous there. The Grey Partridge is not globally threatened (Hoyo *et al.* 1994). However, once a very common farmland bird, it has suffered drastic declines from the late 1950s onwards (by up to 90% over large areas) accompanied by marked range contractions and local extinctions, and is now considered as vulnerable (Tucker & Heath 1994). The ultimate reason for most of the decline is agricultural intensification (Potts 1980).

The Grey Partridge is a typical r-strategy species. Due to high natural predation, it has a short life (*avg.* 1.5 years) and therefore most individuals are able to reproduce only once in their lifetime. As a consequence, its clutch size is the largest recorded for any bird species in the world (*avg.* 15 eggs in Middle Europe up to 20 in the northern part of its range). Second clutches are smaller than first clutches and only produced if the first fails to hatch. After hatching, the partridge family, i.e. covey, stays together until the next spring, when coveys break up whereupon young males leave to form pairs (Glutz von Blotzheim 1973). The pair

bond is very tight; they are probably genetically monogamous. Due to a comparably long paternal care for a bird species, the social bond of the covey is also very strong. Many behavioural features, probably most important, anti-predator behaviour, are learnt from the parents (Dowell 1990, Beani & Dessì-Fulgheri 1998).

The Grey Partridge does not move large distances (the furthest recorded in this study moved 6 km) and is therefore unlikely to re-colonize areas where it has gone extinct. The partridge flies very rarely, mainly on roosting flights during dawn and dusk, or when it has to escape from predators. The roosting places lie preferably in open habitats such as stubbles or ploughed fields (Dowell 1990, pers. observation), probably as a strategy to avoid nocturnal predators, particularly the red fox.

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How do different releasing techniques affect the survival of re-introduced Grey Partridges *Perdix perdix*?

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Abstract

The quality of released individuals can have a significant impact on the success of re-introduction projects. We tested which of the following release techniques resulted in the highest survival of released Grey Partridges *Perdix perdix* in Switzerland; 1) translocation of wild adult birds, 2) release of captive parent-reared adults as family groups and 3) fostering of captive parent-reared chicks to wild barren pairs. Wild hatched offspring (F1 birds) from our re-established breeding pairs served as the control group. We used a multi-state capture-recapture model to estimate monthly survival rates from the data based on monitoring of radio-tagged individuals and reobservation and recovery of ringed individuals. Survival tended to be highest in wild-hatched partridges of the founder population (mean ± SE; 0.90 ± 0.03), followed by that of fostered chicks (0.86 ± 0.03) and translocated adult wild birds (0.82 ± 0.06). While survival of these groups was not statistically different from each other, survival of captive-reared adults was significantly lower (0.70 ± 0.06). We discuss the implication of our results for further partridge re-introduction projects.

INTRODUCTION

Releases of individuals into areas where they have occurred previously (re-introductions), have become an important method to restore locally extinct species (Fischer & Lindenmayer 2000, IUCN Re-introduction Specialist Group 2004). However, many re-introduction attempts have failed because released animals are often highly susceptible to predation or unable to breed successfully (Beck *et al.* 1994, Fischer & Lindenmayer 2000, Wallace 2000). Detailed knowledge about the behaviour and life history of a target species is required to determine the suitable age class, timing and number and source (i.e. captive or wild) of stock for the planned release (Kleiman *et al.* 1986, Miller *et al.* 1994, Sarrazin & Legendre 2000, Green *et al.* 2005).

Different kinds of individuals can be released in re-introduction projects. One commonly used technique is the release of captive-bred individuals, with the advantage that large numbers can be released. However, predator avoidance behaviour is often not well developed in captive bred individuals, as the ability to cope with predators is not only genetically determined but is learnt during parental attention (Menzdorf 1976 & 1977, Dowell 1990, Dobrott 1993, Beck *et al.* 1994, Beani Dessì-Fulgheri 1998). The survival of released individuals may be improved

if they are reared under semi-natural conditions, e.g. parent- or cross-fostering (Sherrod *et al.* 1982, Lewis 1990, Dobrott 1993, Cade & Temple 1995) or if anti-predator behaviour istrained before release (Ellis *et al.* 1978, Hölzer 1999). Another technique is the translocation of wild individuals with the advantage that they have established anti-predator behaviour. Yet survival of these individuals may still be inferior compared to local conspecifics, perhaps because they have no knowledge of local conditions (Church 1993, Sarrazin & Barbault 1996, Stanley Price & Fairclough 1997, Reed 1999). A third release technique is fostering of chicks to wild parents. Captive hatched young are fostered at an early age to wild pairs that failed to successfully produce their own chicks. The advantage of this technique is that young become imprinted and socialized by experienced parents (e.g. predator avoidance), which may enhance their survival (Thomas 1987, Putaala & Hissa 1998). Estimates of survival of individuals released by these techniques are lacking. Such knowledge is important to increase the efficiency of release programs (Brittas *et al.* 1992, Kleiman *et al.* 2000, Meretsky *et al.* 2001).

The threatened Grey Partridge *Perdix perdix* has been the subject of many re-introduction projects throughout its range, either for harvesting purposes or for conservation. These projects have mainly depended on the release of large numbers of pen-reared individuals. The majority of these releases have failed to establish self-sustainable populations, mainly because of severe losses of released individuals due to predation (e.g. Rands & Hayward 1987, Putaala *et al.* 2001, Meriggi *et al.* 2002) and low breeding success (e.g. Rands & Hayward 1987, Church 1993, Putaala & Hissa 1998). We tested whether survival rates of Grey Partridges differed among three different release techniques (translocated wild adults, pen-reared adults, fostered chicks) and compared their merits for establishing a self-sustaining population.

STUDY SITE

We conducted the study in the intensively cultivated Klettgau region (ca 30,000 ha) near Schaffhausen, Switzerland (430 m a.s.l.). Once a common breeding bird in the Klettgau, Grey Partridge populations declined dramatically after 1970 due to a severe loss of unimproved meadows, hedges and embankments, and fallow ground; as well as to an increase of chemical crop protection products and artificial fertilisers (Jenny *et al.* 2002). By 1996 the species was extirpated from the entire Klettgau region (Jenny *et al.* 1998).

Since 1991, the Klettgau has been the target of habitat enhancements by the Swiss Ornithological Institute, which has promoted the sowing of wild-flower strips to recreate an

arable landscape suitable for Grey Partridge. In the most enhanced area of the Klettgau (530 ha), the amount of wild-flower strips had increased from 0 to 13 ha by 2001, the area of hedgerows from 2 ha to 2.7 ha. This area was chosen as study site into which all birds were released. The study area was comprised primarily of cereal grains (49%), oil-seed rape and sunflowers (14%) and root crops (12%). Grassland covered 11%, another 11% was bare of vegetation (e.g. buildings and roads). The field size ranged within 0.1-5.5 ha (for further details see Buner *et al.* 2005).

Several partridge experts judged the habitat quality to be suitable for partridges prior to this release project (see also Buner *et al.* 2005). Between December and February of 1997/98, 1998/99 and 1999/2000, an intensive fox reduction program (shooting foxes with the help of spot lights) was carried out on the study area as well as on an additional buffer zone of approximately 2 km in radius to lower predator pressure. No further predator control was applied.

METHODS

Releases of Grey Partridges

During 1998-2000, we released three different treatment groups totalling 130 partridges in the study area (Table 1), all genetically originating from the western clade of the subspecies *Perdix perdix* (see Liukkonen-Attila *et al.* 2002). The first treatment group was adults caught from different coveys in Germany and the Czech Republic in February (hereafter: translocated wild adults, eight males and 13 females). These birds were kept in pens until they were released in April. Upon release they immediately paired with each other or with individuals released at an earlier stage of the project. By releasing them in spring, we hoped to minimise predation losses during winter. The second treatment group was captive parent-reared adults that were released as family groups (i.e. coveys) in December or January (hereafter: pen-reared adults, 44 males and 33 females in seven coveys). We released them in winter, rather than in spring, because we believe that the adaptation to predators is easier when the birds are still in a covey rather than in pairs. The third treatment group was captive parent-reared chicks that were all successfully fostered at an age of 5-8 weeks in August (hereafter: fostered chicks, N = 32, gender not determined on all birds)to three wild pairs which failed to produce their own chicks. Our control group was comprised of the offspring of successful broods of re-established partridges (hereafter: wild-hatched chicks, N = 67, gender not determined on all birds, five broods).

All released birds were kept in quarantine for at least one month prior to release. Each covey was kept in a separate 4 x 10 m outdoor pen near the study area, containing short grass, sandy areas and bare soil for foraging with tussocky grass and branch heaps for cover. The food provided was a mixture of seeds and pellets with a low dose of Phlubenol added to prevent endogen parasite infections. The day before release, all birds were ringed and moved into release-pens in the study area where they were kept overnight. The pens were opened the following morning. For pen dimensions and the selection of release sites we followed the instructions given by Game Conservancy Limited (1996). All birds used for this study were released in a healthy status, confirmed prior to release by the local veterinarian who analysed blood samples, faeces and measured body weight.

Data collection

During 1998-2001, 113 full-grown individuals were equipped with 10-g radio transmitters (< 3% of body mass) with an expected battery life of eight months and a transmission range of about 3.5 km (Titley Electronics Ltd, Ballina, Australia, Model GPI). The transmitters were mounted using a Rappole harness (Rappole & Tipton 1990) made of 3 mm PTFE (COOK Medical Products, Switzerland, Flat Wound Drain). The transmitters were painted brown to make them less visible. Only adult birds (treatment groups 1 and 2) could be radio-tagged before release. Fostered chicks (treatment group 3) were only ringed, but caught for tagging after they were full grown (60 days after hatching). Wild-hatched birds (control group) were, by definition, individuals without rings, and were eventually caught and ringed when either subadult or adult (Table 1).

Table 1. Number of Grey Partridges released per treatment group in the Klettgau, Switzerland, 1998-2000. Individuals from treatment group 4 were not released but hatched by re-established pairs in the study area and served as control group. The figures in brackets refer to the number of individuals that were radio-tagged.

Treatment group	Total number of birds								Total	
	1998		1999		2000		2001		N	Tagged
1) Wild adults	10	(10)	11	(11)	0	-	0	-	21	100%
2) Reared adults	0	-	0	-	77	(55)	0	-	77	71%
3) Fostered chicks	0	-	8	(7)	24	(7)	0	-	32	44%
4) Wild hatched chicks	15	(8)	0	-	26	(10)	26	(0)	67	27%
Total n / Tagged	25	72%	19	95%	127	57%	26	0%	197	55%

To catch birds we used mist-nets (18.0 x 2.4 m, mesh size 30 mm) set as a large 'funnel' trap (Bub 1991). We approached the birds with two cars to prompt them to walk into the trap. We were able to radio-tag at least one bird in each existing covey or pair on the study area. All radio-tagged birds were located and sighted at least once every week and the total number of birds in each covey or pair was counted. After the mating season, all pairs and singles in the study area were caught, the identity verified and at least one individual per pair was radio-tagged. If an individual was found dead, we noted the cause of death, as assessed by inspection of the carcase.

Under the assumption that individuals which were only ringed did not change their covey or pair (never observed in radio-tagged birds) and given the large effort to count all individuals of each group at least once a week, we could construct encounter histories on a monthly basis for all birds. The information included encounter histories for each individual and month whether it was observed alive with or without a radio transmitter, not observed or found dead.

Estimation of survival

Because of a mixture of radio-tagged (hereafter: tagged) and ringed birds (hereafter: untagged), and because previously untagged birds possibly became tagged or previously tagged birds possibly became untagged (battery dead on radio transmitter), classical methods for the estimation of survival of radio-tagged animals (White & Garrot 1990) were not applicable. Therefore we used a multi-state capture-recapture model (Hestbeck *et al.* 1991, Williams *et al.* 2002) which allowed a separate estimation of survival for tagged and untagged individuals as well as the estimation of the probabilities that birds were tagged and that active tags stopped functioning. We defined a model with five different states at time i: 1) untagged living individuals, 2) untagged dead individuals, 3) tagged living individuals, 4) tagged dead individuals, and 5) living individuals with non-functioning radio transmitters. State transition probabilities are equivalent to the joint probability of survival and changes with the tag status. Specifically, the parameters in the model are S_i, the probability that an untagged individual survives from the beginning of month i to the beginning of month $i+1$, S_i^R the probability that an individual with a tag (active or non-functioning) survives from the beginning of month i to the beginning of month $i+1$, p_i the probability that an individual without or with a non-functioning tag and that is alive at the beginning of month i is relocated in that month, p_i^R the

probability that an individual with an active tag and that is alive at the beginning of month *i* is relocated in that month, r_i the probability that an individual with an active tag that died in the interval *i*-1 to *i* is found at *i*, ψ_i^R the probability that an individual without a functioning tag is caught at the beginning of month *i* and gets a functioning tag, and ψ_i^P the probability that a tag that was active at time *i*-1 became non-functioning at time *i*. The model is written as a matrix of state transition probabilities and a vector of state-specific encounter probabilities. The states of departure (time *i*-1) are in columns, the states of arrival (time *i*) are in rows, the order of states 1 to 5 is from top to bottom and from left to right:

$$
\begin{bmatrix}
(1-\psi^R)S & 0 & 0 & 0 & 0 \\
(1-\psi^R)(1-S) & 0 & \psi^P(1-S^R) & 0 & (1-\psi^R)(1-S^R) \\
\psi^R S & 0 & (1-\psi^P)S^R & 0 & \psi^R S^R \\
\psi^R(1-S) & 0 & (1-\psi^P)(1-S^R) & 0 & \psi^R(1-S^R) \\
0 & 0 & \psi^P S^R & 0 & (1-\psi^R)S^R
\end{bmatrix}
\begin{bmatrix}
p \\ 0 \\ p^R \\ r \\ p
\end{bmatrix}
\quad (1).
$$

The parameters in the model may vary according to the age of the bird, the month treatment group an individual belongs to.

States 2 and 4 ('dead') are absorbing (i.e. individuals that enter one of these states stay there, and can only be re-encountered on the occasion when they enter these states). Because of the low probability of finding dead untagged individuals we decided to define state 2 as unob servable to reduce model complexity. Powell *et al.* (2000) used a similar approach to estimate survival and movement rates from combined mark-recapture and radio-tagging data.

We used program MARK (White & Burnham 1999) to estimate the parameters. However, MARK uses a parameterisation that does not allow us to fit this model directly. With MARK it is possible to estimate only one transition probability for each step of time, hence the product of the parameters we intend to estimate (e.g. $\psi^R S$ for the transition from state 1 (time *i*-1) to state 3 (time *i*) in Equation 1). Yet, we can write the state transition matrix in (1) with two succeeding transition matrices, in which the entries are only single parameters:

$$
\begin{bmatrix}
1-\psi^R & 0 & 0 & 0 & 0 \\
\psi^R & 0 & 0 & 0 & 0 \\
0 & 0 & 1-\psi^P & 0 & \psi^R \\
0 & 0 & 0 & 0 & 0 \\
0 & 0 & \psi^P & 0 & 1-\psi^R
\end{bmatrix}
\begin{bmatrix}
S & 0 & 0 & 0 & 0 \\
1-S & 0 & 0 & 0 & 1-S^R \\
0 & S & S^R & 0 & 0 \\
0 & 1-S & 1-S^R & 0 & 0 \\
0 & 0 & 0 & 0 & S^R
\end{bmatrix}
\quad (2).
$$

The first transition matrix now models the probabilities associated with changes in tag status, the second transition models survival and mortality. Because one step of time is now prolonged into two time steps, the data file was adjusted accordingly: a dummy occasion (a column of zeros) after each real occasion was inserted. Grosbois & Tavecchia (2003) and Schaub & Pradel (2004) provide detailed descriptions and further examples of this modelling technique.

We estimated the 12 monthly survival rates from June (year x) to June (year x+1), because partridge chicks usually hatch in June. Individuals that were known to be alive for >1 year were treated as if they would have been removed from the population at the last observation in year x, and released as a new individual at first encounter in year x+1. This was done to reduce year-specific parameters in the model, although we lost some information about survival and re-encounter probabilities during the time interval without observations. However, as encountering rates were high, this loss of information was regarded as a minor problem.

We assumed that survival rates of partridges that were >3 months old did not change anymore with increasing age. Only fostered chicks and wild-hatched chicks were monitored during the juvenile phase (≤3 months old), all other birds were only monitored during the adult phase (i.e. they were >3 months old). We did not consider a relative age effect, i.e. the change of survival as a function of time after release. Thus, a time effect in the model denotes variation of survival between specific times of the year.

A critical assumption for our data was that all individuals were independent from each other (Lebreton *et al.* 1992). Due to the fact that Grey Partridges live in either coveys or pairs throughout the year, this assumption was unlikely to be met. Non-independence of individuals (overdispersion) does not lead to biased parameter estimates, but the standard errors of the estimates are underestimated which affects model selection and inferences from the data (Anderson *et al.* 1994). Standard errors could be adjusted for overdispersion if the overdispersion coefficient, $\hat{c}$, could be estimated, but this was not possible for our specific model. In order to get a rough estimate of overdispersion, we removed the recoveries of all dead birds in our data set (i.e. as if they had never been found), and assumed that resighting rates of the birds were similar regardless of whether they had a functioning tag, a non-functioning tag, or were untagged. This was justified *a posteriori* by the high and similar resighting rates of tagged and untagged birds (se Results). Further, we assumed that the tag had no effect on survival. The original data set became a single-state capture-recapture data

set for which a goodness-of-fit (GOF) test is available and an estimate of $\hat{c}$ can be obtained (Lebreton *et al.* 1992). We tested the goodness-of-fit for a model with time and treatment group specific survival and recapture rates with program U-CARE (Choquet *et al.* 2001). The GOF did not indicate significant lack of fit ($\chi^2_{14} = 18.90$, $P = 0.17$). The variance inflation factor is estimated to be $\hat{c} = 1.35$ ($\hat{c} = \chi^2/\text{df}$; Lebreton *et al.* 1992). This estimate of $\hat{c}$ is an approximation only. To evaluate whether our inferences from model selection are robust with respect to different estimates of $\hat{c}$ we also considered more conservative values for $\hat{c}$ (2.0, 3.0, 4.0).

We followed the model selection strategy recommended by Burnham & Anderson (1998). We defined *a priori* a set of possible candidate models and used the quasi-likelihood adjusted Akaike Information Criterion corrected for small sample sizes (QAIC$_c$) to rank the models according to their support by the data. Because we localised the tagged individuals and tried to see individuals without active tags at least once every week throughout the year and because we pooled the data into monthly periods, we could confidently assume that the probabilities of relocalising, resighting and recovering (p, p^R, r) the birds did not vary over the year. By contrast, the probability that a bird without a functioning tag would receive a functioning tag (ψ^R) varied, because we only made an effort to catch the birds during specific periods. Also, the probability that a functioning tag would become non-functioning due to battery failure (ψ^P) was always kept time-dependent.

The most complex model for the monthly survival considered a separate estimate for each of the four treatment groups in each month, separate survival rates of the juvenile (≤ 3 months) and older birds, and an additive tag effect (Putaala *et al.* 1997, Bro *et al.* 1999). This model is denoted by S$_{[R+g*a*t]}$, where R refers to tag effect, g to treatment group effect, a to age effect, and t to time effect. We considered several simpler models which either assumed additive time effects on all treatment group and age combinations (referring to the hypothesis that all treatment groups are affected in the same way by environmental variation), no time-effect at all (referring to the hypothesis that variation between the monthly survival rates was marginal), additive effect of treatment group on age (referring to the hypothesis that the treatment effect was the same in both age classes), without treatment effects (referring to the hypothesis that survival does not differ among treatment groups), and combinations thereof. We also considered all these models with and without an additive tag effect. In total, we fitted 14 models.

RESULTS

Survival

Model selection clearly showed that survival differed among treatment groups. Models without treatment effect were consistently lower ranked than models with treatment effects (Table 2). It also appeared that there was low support for a significant temporal variation in survival, and some evidence for an effect of tag on survival. If larger values of $\hat{c}$ are considered, the ranking of the models changes slightly, but the main conclusions remain. In particular, the best ranked model was always one with a treatment group effect, and the sum of the Akaike weights of all models containing a group effect on survival was always >0.7, irrespective of the chosen $\hat{c}$ (Table 3). This suggests that our conclusions regarding the effect of treatment group on survival are robust. More uncertainty existed with respect to the effect of tag on survival. For large values of $\hat{c}$, the best ranking models did not contain a tag effect (Table 3). Because the main inferences were not strongly dependent on $\hat{c}$, subsequent inferences are based on $\hat{c} = 1.35$.

Table 2. Modelling survival rates (S) of released Grey Partridges (Klettgau, Switzerland, 1998-2000), based on the most complicated model $\{S_{[R+g*a*t]},\ \psi_t^R,\ \psi_t^P,\ p,\ p^R,\ r\}$ and simplifications thereof. For each model the number of estimated parameters, the quasi-likelihood adjusted relative deviance, the difference of the small sample size and quasi-likelihood adjusted Akaike Information Criterion ($\Delta QAIC_{ci}$ = $QAIC_{ci}$-$QAIC_{cmin}$), and the Akaike weight [w_i = $exp(-0.5\Delta QAIC_{ci})/\Sigma(exp-0.5\Delta QAIC_{ci})$] are shown. Subscript R refers to the radio-tag effect, subscript g to the treatment group effect, subscript a to an age effect, and subscript t to a time effect. Model selection was based on a variance inflation factor of $\hat{c}$ =1.350. Since only the model structure of the survival parameters differ among the candidate models, we only show this part of the model notation.

Model	Number of. parameters	QDeviance	$\Delta QAIC_c$	$QAIC_c$ weight
$S_{[R+g*a]}$	28	6586.9	0.00	0.50
$S_{[R+g+a]}$	27	6590.9	1.94	0.19
$S_{[g*a]}$	27	6591.2	2.16	0.17
$S_{[g+a]}$	26	6595.0	3.85	0.07
$S_{[g*a+t]}$	38	6571.1	5.96	0.03
$S_{[g+a+t]}$	37	6574.9	7.57	0.01
$S_{[R+g*a+t]}$	39	6570.6	7.65	0.01
$S_{[R+g+a+t]}$	38	6574.5	9.36	0.00
$S_{[R+a]}$	24	6608.3	12.95	0.00
$S_{[R+a+t]}$	35	6586.9	15.17	0.00
$S_{[a+t]}$	34	6589.3	15.35	0.00
$S_{[g*a*t]}$	73	6509.4	24.59	0.00
$S_{[a]}$	23	6622.9	25.36	0.00
$S_{[R+g*a*t]}$	74	6509.0	26.61	0.00

Table 3. Comparison of model selection with different values of the variance inflation factor $\hat{c}$. Shown are the Akaike weights of the corresponding models and the sum of the Akaike weights of all 10 models containing a treatment group effect, and of all seven models containing a radio-tag effect. For model notation see Table 2.

Model	$\hat{c}$ = 1.35	$\hat{c}$ = 2.0	$\hat{c}$ = 3.0	$\hat{c}$ = 4.0
$S_{[R+g*a]}$	0.50	0.33	0.19	0.12
$S_{[R+g+a]}$	0.19	0.24	0.22	0.17
$S_{[g*a]}$	0.17	0.23	0.21	0.17
$S_{[g+a]}$	0.07	0.18	0.26	0.26
$S_{[g*a+t]}$	0.03	0.00	0.00	0.00
$S_{[g+a+t]}$	0.01	0.00	0.00	0.00
$S_{[R+g*a+t]}$	0.01	0.00	0.00	0.00
$S_{[R+g+a+t]}$	0.00	0.00	0.00	0.00
$S_{[R+a]}$	0.00	0.02	0.11	0.23
$S_{[R+a+t]}$	0.00	0.00	0.00	0.00
$S_{[a+t]}$	0.00	0.00	0.00	0.00
$S_{[g*a*t]}$	0.00	0.00	0.00	0.00
$S_{[a]}$	0.00	0.00	0.01	0.06
$S_{[R+g*a*t]}$	0.00	0.00	0.00	0.00
Σ(models with g)	0.98	0.98	0.88	0.72
Σ(models with R)	0.70	0.59	0.52	0.52

Based on the most parsimonious model ($S_{[R+g*a]}$), estimates of encountering Grey Partridges were high (p = 0.96 [95% confidence interval: 0.93 – 0.98], p^R = 0.99 [0.95 – 1.00], r = 0.80 [0.68 – 0.88]), reflecting our intense monitoring efforts. The probability that an untagged individual became tagged varied among months from 0.04 (95% confidence interval: 0.01 – 0.20) to 0.41 (95% confidence interval: 0.27 – 0.58), and the monthly tag failure rate varied from 0.00 to 0.29 (95% confidence interval: 0.07 – 0.67).

Mean monthly survival rates were highest for adult Grey Partridges that hatched in the study area (control group) and lowest for captive-reared adult Grey Partridges (Figure 1). To test *a posteriori* which group of adult Grey Partridges had different monthly survival rates, we fitted two more models. In the first we considered adult survival of wild-hatched and fostered adult individuals to be the same. This model (number of parameters = 27; QDeviance = 6587.18) was better than the best model so far (ΔQAICc = -1.826). Next, we fitted a model in which survival rates of wild-hatched, fostered, and translocated wild adults were the same. This model (number of parameters = 26; QDeviance = 6589.07) became even more parsimonious (ΔQAICc = -2.066). Given that the model without survival differences among groups was clearly worse (Table 2), the main difference between these four treatment and control groups was survival of pen-reared adults, which was clearly lower than survival of birds from the other groups. Within the primary treatment groups, fostered chicks tended to

have the highest survival rate. This conclusion also held for other values of $\hat{c}$.

Fig. 1. Probabilities of monthly survival of different groups of released Grey Partridges (Klettgau, Switzerland, 1998-2000) estimated with the most parsimonious model $\{S_{[R+g^*a]},\ \psi_t^R,\ \psi_t^P,\ p,\ p^R,\ r\}$. Light grey bars refer to birds without radio-tags, white bars to birds with radio-tags. The cross hatched bars indicate birds of the control group (wild-hatched individuals in the study area). The vertical lines show the limits of the upper and lower 95% confidence interval of the estimates ($\hat{c}$ =1.350). * This survival estimate of untagged translocated birds was predicted by the model, since there were no data within this group. Juvenile survival refers to the period between the age of two months and three months.
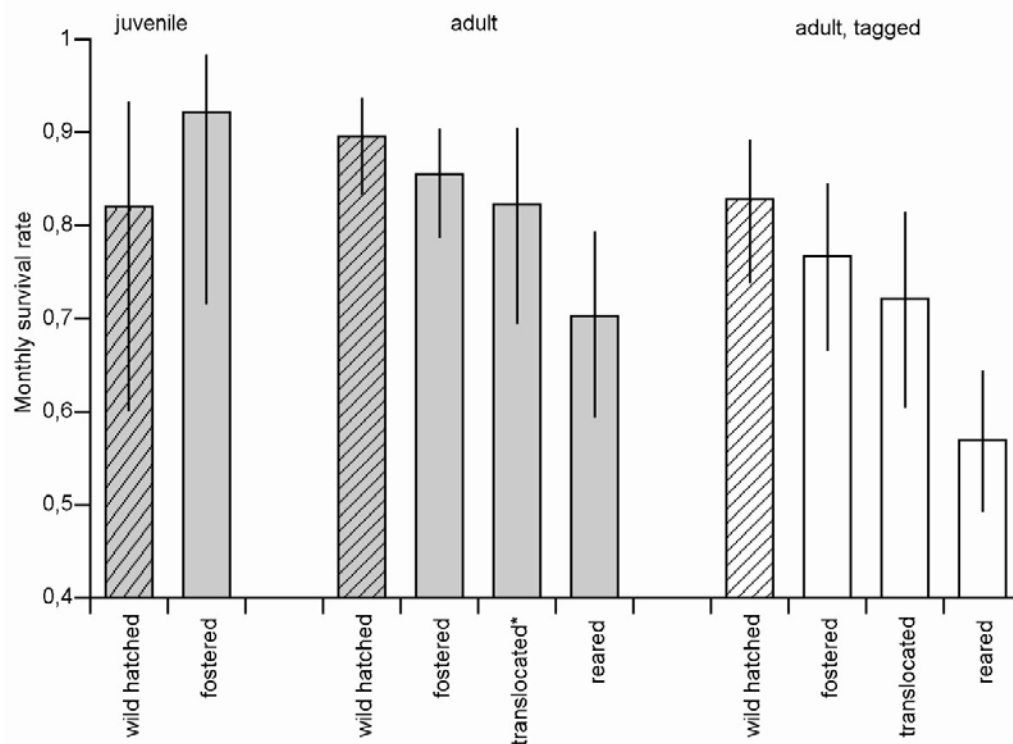
The monthly juvenile survival of wild-hatched partridges appeared to be lower than that of their fostered conspecifics. However, this was because estimated juvenile survival of wild-hatched birds was calculated as an average rate over the first three months of life (from hatching to the age of three months), whereas juvenile survival of fostered birds refers to individuals from an age of two months. To obtain comparable estimates, we reran the *a priori* best model, but considered time(age)-dependent survival rates for wild-hatched juveniles.

Monthly survival of wild hatched juveniles from hatching to an age of one month was 0.58 [SE = 0.08], from the age of one month to the age of two months 0.88 [SE = 0.06], and from the age of two months to an age of three months 0.82 [SE = 0.08]. This last estimate

corresponds to birds at the same age as the fostered juveniles (0.92 [SE = 0.06]); and is not significantly lower (z = -1.01; P = 0.16). The survival rates of tagged individuals was slightly lower than survival rates of individuals without tags (difference on the logit scale: -0.58 [SE = 0.28]).

Causes of death

We found the carcasses of 85 partridges; 82 of them had apparently been killed by predators, one died from disease, one died in a traffic accident and one died as a result of a territorial fight. Predation by mammals was more frequent (46 in total; 36 by red fox *Vulpes vulpes*, and 10 by domestic cat *Felis catus*) than predation by avian predators (24 in total; 20 by common buzzard *Buteo buteo*, three by sparrowhawk *Accipiter nisus*, and one by a wintering hen harrier *Circus cyaneus*). All four treatment and control groups of partridges suffered from mammalian and avian predators in similar proportions (χ^2_3 = 2.92, P = 0.40).

DISCUSSION

Our study provides evidence that survival probability of released partridges depends on release strategy. While the survival rate of the fostered chicks and translocated wild adults was not different from survival of wild-hatched chicks (control, offspring of established pairs), survival of pen-reared adults was significantly lower.

The difference in monthly survival rates between pen-reared adults (S = 0.718, SE = 0.055) and the mean of the other groups (S = 0.870, SE = 0.025) may appear marginal. However, the mean life expectancy (Seber 1982) of the pen-reared adults (3.01 months, SE = 0.26) is less than half that of the other groups (7.16 month, SE = 1.48). This difference is biologically important, because longer-living individuals accumulate more experience and are therefore more likely to reproduce successfully, or if not, may at least serve as foster parents. Because the main cause of mortality in partridges is predation (this study, e.g. Potts 1986), the different survival skills of the three treatment groups is probably due to differential experience in avoiding predators (Dowell 1990). While pen-reared adults have not normally encountered predators prior to release and are not familiar with their release habitat, translocated wild birds have the advantage of being at least familiar with predators. Chicks reared in captivity and fostered to wild counterparts benefit from the behavioural skills of their experienced parents by acquiring knowledge of both, predator avoidance and local habitat. Survival rates of our

wild-hatched chicks were similar to wild (not re-introduced) partridge populations (Panek 1992, Potts & Aebischer 1994, Panek 1997, Putaala 1997, Bro *et al.* 1998).

The radio-tags may have had a minor negative effect on partridge survival (8-19% lower; inference based on the best model). However, the summed QAIC weight of models with and without radio transmitters is nearly the same when $\hat{c} > 2$, reflecting considerable uncertainty about a radio-tag effect on survival (Table 3). Bro *et al.* (1999) found a negative impact of necklace mounted radio-tags on partridge survival and Putaala *et al.* (1997) showed that flight abilities of Grey Partridges were reduced when they were equipped with a backpack radio-tag. To avoid those reported adverse effects we used a Rappole-harness (Rappole & Tipton 1990). Further studies with larger sample sizes are required to clearly demonstrate the effect of radio-tags on survival. Survival may also be affected by other factors such as environmental variation among years or gender; neither of which was considered here.

To compare the efficiency of our three different release techniques we calculated the number of individuals that need to be released in each treatment group for obtaining a population of 20 individuals in May, based on the estimated group-specific survival rates (Table 4). Only 24 translocated wild adults have to be released in April (one month before the breeding season starts) to reach the goal. However, translocations are often problematic because they can have negative effects on the source population (IUCN Re-introduction Specialist Group 2004). This is of special concern because partridges are considered vulnerable throughout Europe (Tucker & Heath 1994). Despite its efficiency we therefore regard translocation of many partridges as not advisable.

The efficiency of the two release techniques using pen-reared individuals is remarkably different. Although pen-reared adults are released later than fostered chicks, about twice as many individuals must be used to obtain the same number of potential breeders in the next year (see Table 4). Importantly, when compared to the fostered birds, the low survival rates of the pen-reared adults indicate that approximately 90% fewer birds are still alive at the beginning of the second breeding season. Therefore, we conclude that fostering captive reared chicks is the best release regime given that it has no negative impact on existing wild partridge populations.

The establishment or re-establishment of a self-sustaining population is the basic aim of re-introduction projects (Scott & Carpenter 1987). To evaluate the self-sustainability of populations created by different releasing regimes it is necessary to study the breeding performance of the different groups of birds in addition to survival. We monitored breeding

success of the released and wild-hatched Grey Partridges of the founder population and found that individuals of all treatment groups were able to reproduce successfully. However, because of the small sample size, we could not test for differences in breeding performance among the treatment groups. Therefore further studies that assess, in more detail, whether the reproductive skills of the treatment groups differ would be highly valuable. Having this information, the next step would be to include information about the economic costs to identify the most efficient release strategy.

Table 4. Hypothetical number of individuals that need to be released in each group (in the control group it is the number of hatchlings of re-established pairs) to obtain a population of 20 individuals at time of reproduction (May in year t). Indicated is also the number of individuals alive at the beginning of the second breeding season. Calculations are based on the survival estimates from the best model (see Table 2) and refer to untagged individuals. The standard errors are in brackets.

Group	Release month	Number to be released	Number alive in May (year t+1)
Translocated wild adults	April (year t)	24.3 (1.8)	1.9 (1.7)
Pen-reared adults	December (year t-1)	116.5 (9.8)	0.3 (0.3)
Fostered chicks	August (year t-1)	65.2 (18.5)	3.0 (1.4)
Wild-hatched chicks	June (year t-1)	147.5 (47.9)	5.3 (2.1)

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Ecologically enhanced areas – a key habitat structure for re-introduced Grey Partridges *Perdix perdix*

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Abstract

We analysed the spatial distribution of home-ranges and the habitat use of re-introduced Grey Partridges *Perdix perdix* in relation to newly established ecologically enhanced areas, i.e. wild-flower strips and hedges, within an intensively cultivated area in Switzerland from which the species had become extinct. All birds settled within c. 30% of the study area where the proportion of enhanced areas was highest (5.8%). At the level of the individual family group, we found a significant over-proportional use of enhanced areas throughout the year. Furthermore, when the birds used the agricultural fields, the use densities strongly declined with distance from the nearest enhanced area. Thus, the availability and spatial distribution of ecologically enhanced areas were the main determinants of the partridges' range use. These results indicate that a framework of ecologically enhanced areas is a key habitat structure for Grey Partridges, and that these enhancements, even if small in proportion, were the crucial first measure to restore the research area to an appropriate Grey Partridge habitat, and thus, the basis for successful re-introduction in this intensively cultivated area.

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INTRODUCTION

The continuing decline of Grey Partridge *Perdix perdix* populations on a European scale (Haagemeijer & Blair 1997) illustrates that the impact of conservation measures for this highly vulnerable 'flagship' species is not yet satisfactory (e.g. Potts 1997, Sotherton 1998, Schifferli 2000, Game Conservancy Limited 2001). Although the causes of the population declines have been intensively investigated (e.g. Tucker & Heath 1994, Potts & Aebischer 1995, Hagemeijer & Blair 1997, Putaala & Hissa 1998, Bro *et al*. 2000a), it is unclear whether and to what extent ecological enhancement measures may restore abandoned areas for eventual re-colonisation.

The local breeding density of Grey Partridges is positively correlated with the availability of perennial plant cover, such as shrubs or herbaceous stands (e.g. Rands 1986, Chiverton 1999, Panek & Kamieniarz 2000). The species nests preferentially in such structures (e.g. Potts 1986, Rands 1986, Panek 2002) since these provide both high food availability and protection against predators. The abundance of invertebrate food is particularly important for chick survival and thus, reproductive success (e.g. Green 1984, Potts 1986, Panek 1997, Liukkonen-Anttila *et al.* 2002). This suggests that establishing ecologically enhanced areas in intensively cultivated regions improves the availability of both suitable nesting habitat and food resources (e.g. Blake & Dowell 1992, Moreby & Aebischer 1992, Bro *et al.* 2000 b,c;

Panek & Kamieniarz 2000). However, it is unclear whether a framework of enhanced areas covering only a small proportion of an intensively cultivated area may provide the necessary and adequate resources for the partridges' entire life cycle, and thus, allow for re-colonisation.

In this study, we analyse how re-introduced Grey Partridges responded to the pattern of ecologically enhanced areas, i.e. wild-flower strips and hedges, within an intensively cultivated agricultural landscape in Switzerland from which the species had become extinct. In particular we analyse the importance of ecologically enhanced areas for the birds' range use throughout the year. Two main aims are addressed: 1. We analyse whether the released birds settled selectively in areas with a high proportion of ecologically enhanced areas. 2. We assess the relevance of ecologically enhanced areas for the birds' range use and habitat selection within the home-ranges in relation to the seasonal changes of vegetation structure, and to cultivation. Therefore, the main conservation issue is to test whether the implemented compensation measures were a successful first step in the re-introduction process in that they provided the vital resources allowing released Grey Partridges to establish home-ranges in a formerly unsuitable habitat. The survival and reproductive performance of the re-introduced birds as the measures of long-term success of re-introduction will be analysed elsewhere.

STUDY SITE

We conducted the study in the Klettgau region near Schaffhausen, Switzerland (430 m a.s.l.). The study area (c. 530 ha) is intensively cultivated, mainly for growing cereals (49%), oil-seed rape and sunflowers (14%) and root crops (12%). Grassland covered 11%, another 11% were bare of vegetation (buildings, roads etc). Permanent cover such as wild-flower strips, hedgerows and grass banks amounted to 3% of the area. The field size ranged from 0.1 to 5.5 ha (Fig. 1). Since 1991, the whole study area has been subject to ecological enhancements, particularly by promoting sown and spontaneous wild-flower strips. From 1991 to 2001 the area of wild-flower strips increased from 0 ha to 12 ha, the area of hedgerows from 2 ha to 2.7 ha (for a detailed description see Jenny *et al.* 2002). The Grey Partridge was once a common breeding bird in the Klettgau region. However, the population declined dramatically after 1980 due to the removal of natural structures such as unimproved meadows, hedges and other ecotones. Despite the initiation of ecological enhancements in 1991, the last wild partridges in the study area were observed in 1992 (Jenny *et al.* 1998).

METHODS

Release of Grey Partridges

From 1998 to 2000 we released 142 partridges (10 adult individuals in 1998, 23 adults and 8 chicks in 1999 and 77 adults and 24 chicks in 2000, release sites see Fig. 1). Entire family groups (coveys) were released between mid December and mid March, adult pairs in mid April. Taking advantage of the fact that pairs having lost their brood easily adopt 'foster' chicks (Schöfl 1958, Szederjei *et al.* 1959) we released juvenile partridges at an age of c. 8 weeks in August at sites where pairs without chicks were observed. All 32 released partridge chicks were successfully adopted by those adults. Although we attempted to release as many wild caught birds as possible, we obtained only 33 wild partridges (22 of German and 11 of Czech origin). The rest of the birds originated from rearing stations (77 adults from France and 32 chicks from Switzerland) where they were parent-bred under near-natural conditions. Groups were kept separately in 16 m^2 pens offering bare soil, mown and high vegetation (see also Thomas 1987, Putaala & Hissa 1998). Before releasing, all birds were kept in quarantine for one month. Each covey (i.e. parents with their chicks) was kept in a separate pen near the study area. The day before release, we moved the birds into release-pens in the study area where they were kept overnight, then pens were opened in the following morning. For pen dimensions and the selection of releasing sites we followed the instructions given by Game Conservancy Ltd (1996).

Data collection

A total of 110 adult birds were equipped with a 10-g radio-tag (< 3% of body mass) of an expected life-time of eight months and a transmission range of c. 3.5 km (Titley Electronics Ltd, Ballina, Australia, Model GPI). The tags were mounted using a Rappole-harness (Rappole & Tipton 1990) made of 3 mm PTFE tubing originally used for surgery purposes (COOK Medical Products, Switzerland, Flat Wound Drain). The tags were painted brown and thus were virtually invisible.

To catch birds that had hatched in the study area we used a large 'funnel' trap (Bub 1991) made of mist-nets (18.0 by 2.4 m, mesh size 30 mm). We approached the birds with two cars to prompt them to walk into the trap.

The collection of the data used in this analysis started one month after release and continued as long as one transmitter per family group was working or until the break-up of a group. Since the range use of unmated birds is likely to differ considerably from that of pairs

and coveys (O'Gorman & Kavanagh 2002), we excluded single birds from the analysis. The birds were located by 'homing in' (Kenward 2001) using a three-element hand-held Yagi antenna. To avoid disturbing the birds we tried to locate and spot the birds from a car (47% of all cases). If the visual observation failed, we located the birds by triangulation from two different positions at c. 10-50 m from the birds. Locations were noted on a 1:5000 map and later digitised using Arc View GIS 3.2. The number of partridge groups (pairs or coveys) observed and sample sizes for each time period are listed in Table 1.

Table 1. Sample size and number of radio-locations for each seasonal period.

Time period	Observation period	Number of groups (pairs or coveys)	Observation days per group	n locations per group	
			Avg±S.D.	Min	Max
spring	01.03.-30.04.	9	30.3 ± 13.7	26	90
summer	01.05.-31.07.	11	47.5 ± 26.4	32	456
late summer	01.08.-15.09.	5	30.0 ± 3.7	86	199
autumn	16.09.-31.10.	5	30.0 ± 3.4	100	129
winter	01.11.-27.02.	5	51.6 ± 16.7	92	234

Data pooled over three years (1998-2000).

Each group was located 1-4 times daily, depending on the number of birds under observation. The observation sessions were distributed randomly over daytime with a minimum of one hour between two consecutive locations of the same group. In addition to the location we noted the vegetation type and height and the birds' activity at that time.

We defined 12 categories of vegetation types including hedgerows and wild-flower strips (ecologically enhanced areas), meadows and embankments, and cultures such as cereals, root crops, maize and sunflowers (non-enhanced areas, listed in fig. 3). Wild-flower strips were narrow strips of 6-20 m width along field edges and were initially sown with a mixture of c. 30 wild plant species, and were maintained for at least six years (for detailed descriptions see Nentwig et al. 1998; Jenny et al. 2002). A total of 234 plant species were recorded in the wild-flower strips in the research area (Ullrich 2001). Several investigations have demonstrated that the diversity of insect species in such strips is also very high (for an overview see Reisner et al. 1997). The spatial pattern in habitat types was mapped using Arc View GIS 3.2. The height of the vegetation was estimated as the average of 10-30 measurements (to the nearest 10 cm) per category that were taken at different sites. Five

seasonal periods were defined according to the most influential farming activities such as ploughing and harvesting. The *spring* period started when the last stubble fields and intermediate crops were ploughed and ended after all crops were sown. The *summer* period lasted until the harvest of all winter cereals, *late summer* until the harvest of sunflowers, *autumn* until the harvest of the last crops, i.e. sugar beet, and *winter* lasted from harvesting of the last crops until ploughing started in spring (see also Table 1).

Statistical Analyses

Since partridge group members keep very closely together, the unit for all analyses was the family group, that is, a pair with or without chicks, depending on the season. Each location therefore included several individuals of which at least one was radio-tagged. We calculated group home-ranges using fixed kernel estimation (Spatial Analyst tool, ArcView GIS 3.2, cell size 20m, radius 50m) and denoted the contour covering 95% of the density distribution as the home-range area.

Following Aebischer *et al.* (1993) we evaluated habitat use by a 2-step process using compositional analysis. First, we compared the proportions of enhanced and non-enhanced areas in the group home-ranges to the proportion available in the study area. In the second step we analysed the distribution of radio-locations in relation to the availability of all habitat types within the home-ranges. We followed Aebischer *et al.* (1993) for the substitution of missing values by a small proportion, i.e. 0.01%, for available but unused habitat types. The use densities were tested applying randomisation tests according to Edgington (1980) on a basis of 999 randomisations. Log-ratio differences were tested using Wilk's lambda, λ, according to Chatfield & Collins (1980). When the overall distribution of locations differed significantly from the proportions available ($P < 0.05$), we used pairwise tests to rank the habitat types according to the relative use densities (Aebischer *et al.* 1993). All statistical tests were carried out using a GENSTAT procedure provided by N. Aebischer (Aebischer *et al.* 1993; Genstat 5 Committee 1987).

Since animals typically move in non-random trajectories, consecutive locations are serially correlated. This, however, does not impose problems in kernel and compositional analyses. A more important issue is that the over-all sample size and observation periods are sufficient to represent the animal's range use and resource selection appropriately. Kernel procedures are non-parametric. De Solla *et al.* (1999) have shown that eliminating serial correlation reduces the accuracy of home-range estimates. For compositional analysis, serial correlation of

subsequent locations is irrelevant because the single location is not used as an independent replicate. The location sample is the basis to calculate a set of estimates of proportions of fixes in the different types of resources. Therefore, the correct degrees of freedom representing the number of experimental units (the family groups) is used (Hurlbert 1984). The non-independence within this composition of proportions is accounted for by the log-ratio transformation used in compositional analysis. The critical point in this type of analysis is that the animal's degrees of freedom in relation to resource selection should be unrestricted. Therefore we selected the minimum intervals between consecutive locations such that the birds could have changed to any other resource within their home-range (White & Garrott 1999). The median distance between two consecutive fixes of one family group was 84.3 m (lower/upper quartile 40.5 and 173.3 m), indicating that the birds were rarely relocated consecutively in the same habitat element of their home-range.

RESULTS

Settlement and home-range size

Of the 110 released and radio-tagged adult partridges, 80 birds remained within the study area and 57 survived the first month after release. During the first month after release, we observed frequent movements across the whole research area. Data from this period of settlement were excluded from the analysis. After settling, 98% out of a total of 4348 locations were recorded in only c. 30% of the study area where the density of enhanced areas was maximal (Fig. 1). The proportion of ecologically enhanced areas in the range where partridges settled (i.e. within the 98% contour) was 5.8% whereas the proportion in unused parts of the study area was 1.1%.

The size of the group home-ranges varied significantly with season. In spring (pre-breeding period) and summer (breeding period), the average group home-ranges ($\pm$S.D.) were 6.8 ($\pm$ 4.0) ha and 6.9 ($\pm$ 2.6) ha, respectively. From late summer until the end of winter (non-breeding period), the home-ranges were significantly larger (late summer: 15.2 ($\pm$ 6.6) ha; autumn: 17.0 ($\pm$ 4.0) ha; winter: 14.4 ($\pm$ 3.6) ha). The variation in the number of locations did not affect home-range estimates significantly (ANCOVA, overall $r^2_{adj.} = 0.49$; Period: $F_{4,28} = 9.0$, $P<0.001$, n of locations: $F_{1,28} = 0.32$, $P = 0.58$, Fig. 2).

Fig 1. Map of the study area indicating the distribution of ecologically enhanced areas in 2000. The grey contour line includes 98% of the radio-locations obtained during the first month after release, i.e. the settlement period (n = 1274); the black contour line includes 98% of the radio-locations obtained after settlement from 1998-2000 (n = 4348). The stars indicate the release sites, ecologically enhanced areas are given in red, human settlements are given in grey.
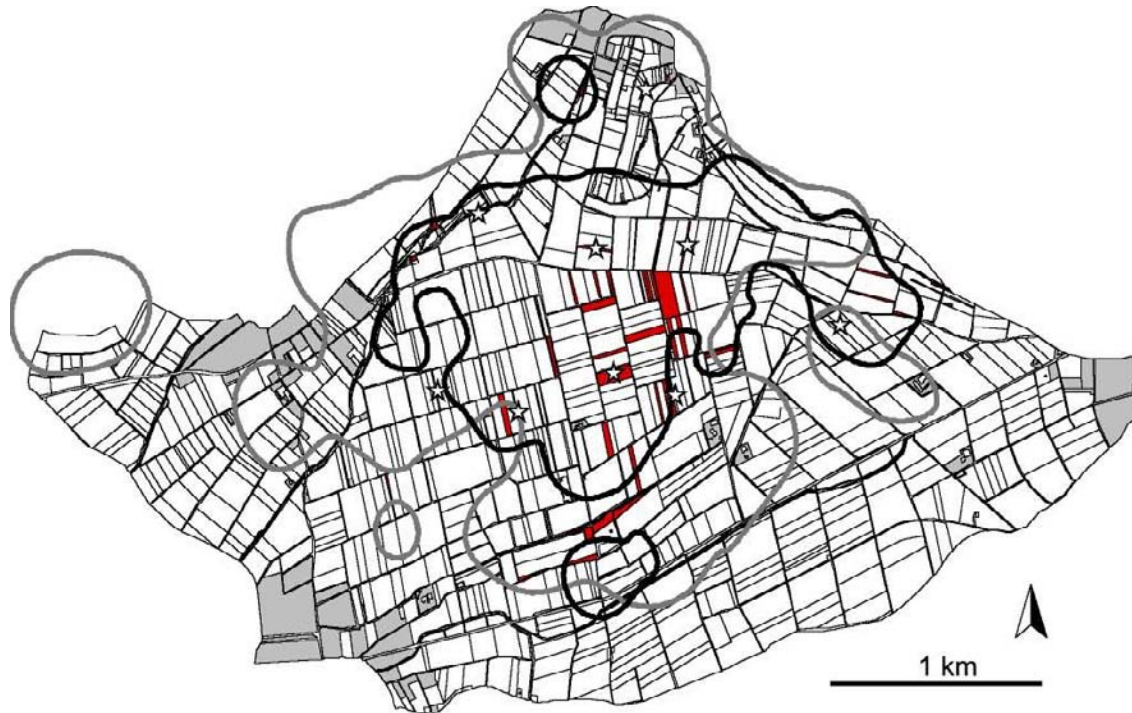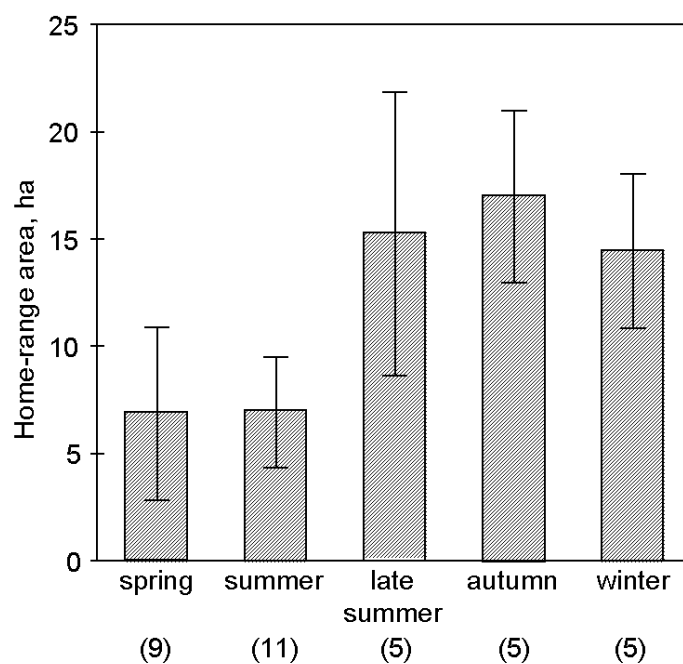

Fig 2. The size of Grey Partridge group home-ranges as revealed by radio-tracking in 1998-2000. Means and SD are given. Numbers in brackets indicate the no. of groups.

Habitat use

Relative use of ecologically enhanced areas

For all five periods, the proportions of enhanced and non-enhanced areas within partridge home-ranges differed significantly from the proportions available in the whole study area (spring: $\lambda = 0.41$, $P = 0.035$; summer: $\lambda = 0.61$, $P = 0.033$; late summer: $\lambda = 0.12$, $P = 0.05$; autumn: $\lambda = 0.31$, $P = 0.05$; winter: $\lambda = 0.08$, $P = 0.05$; sample sizes are given in Table 1). The ranking matrix is given in Table 2. In all periods, the home-ranges included a significantly higher proportion of enhanced areas compared to the availability of enhanced areas across the study area.

Except in late summer, the proportions of radio-locations in enhanced and non-enhanced areas, differed significantly from the proportions available within the respective home-ranges, indicating a markedly over-proportional use of enhanced areas (spring: $\lambda = 0.20$, $P = 0.003$; summer: $\lambda = 0.23$, $P = 0.001$; late summer: $\lambda = 0.93$, $P = 0.87$; autumn: $\lambda = 0.05$, $P = 0.05$; winter: $\lambda = 0.069$, $P = 0.05$; for sample sizes see Table 1). The ranking matrix is given in Table 2.

These results indicate that both the spatial distribution of partridge group home-ranges and the habitat use within these were strongly affected by the availability of ecologically enhanced areas.

Table 2. Rank orders of vegetation types as obtained from compositional analysis of radio-locations compared to the proportion available within group home-ranges. The duration of time periods and sample sizes are given in table 1. enhanced: wild-flower strips and hedges, non-enhanced: total of all other available vegetation types. >>> denotes a significant deviation, > a non-significant deviation from proportionality at $P < 0.05$. Where the enhanced vegetation type is used significantly more than non-enhanced, this is marked in bold.

Periods	Rank orders					
	home ranges vs. total area			locations vs. home ranges		
spring	**enhanced**	>>>	non-enhanced	**enhanced**	>>>	non-enhanced
summer	**enhanced**	>>>	non-enhanced	**enhanced**	>>>	non-enhanced
late summer	**enhanced**	>>>	non-enhanced	enhanced	>	non-enhanced
autumn	**enhanced**	>>>	non-enhanced	**enhanced**	>>>	non-enhanced
winter	**enhanced**	>>>	non-enhanced	**enhanced**	>>>	non-enhanced

Table 3. Rank orders of vegetation types as obtained from compositional analysis of radio-locations compared to the proportion available within group home-ranges. The duration of time periods and sample sizes are given in table 1. w-f strips: wild-flower strips, tracks: tracks across the fields,

Periods	Rank orders								
	1		2		3		4		5
spring	**hedges**	>>>	rape	>>>	w-f strips	>	cereals		tracks
summer	**w-f strips**	>>>	tracks	>>>	sunflowers	>	grassland	>	cereals
late summer	sunflowers	>	**w-f strips**	>>>	maize	>	stubbles	>	grassland
autumn	**w-f strips**	>	stubbles	>>>	maize	>	rape	>	tracks
winter	**hedges**	>>>	**w-f strips**	>>>	rape	>	stubbles	=	int. crops

Overall habitat use within home-ranges

Except in late summer, the proportions of radio-locations in all vegetation types differed significantly from the proportions available in the respective home-ranges (spring: $\lambda = 0.16$, $P = 0.003$; summer: $\lambda = 0.15$, $P = 0.002$; late summer: $\lambda = 0.059$, $P = 0.10$; autumn: $\lambda = 0.02$, $P = 0.05$; winter: $\lambda = 0.002$, $P = 0.05$). The observed proportions (study area; home-range, locations) are given in Fig. 3, the resulting ranking matrix is given in Table 3. Due to the large variance between home-ranges, statistical tests for between-rank differences revealed significant results only for the most used categories. In all seasons the relative use of the two top-ranked vegetation types was significantly higher compared to the rest of the vegetation types. Compared to the proportion available, wild-flower strips and hedges were highly preferred vegetation types. However, there were remarkable seasonal differences. In all periods, the proportion of locations in wild-flower strips was 3 to 9 times higher than expected from proportional use. A strongly different pattern was found for hedges. During winter and spring, hedges were even more used than wild-flower strips, with ratios of observed to available proportion of 6-9. However, from summer to autumn, hedges remained virtually unused. Besides wild-flower strips and hedges, a significant over-proportional use was only found for sunflower fields in late summer and stubble fields in autumn.

Distribution of locations in relation to vegetation height

In summer, 63% of the home-ranges were covered with vegetation higher than 0.5 m, whereas this proportion was only 4.5% during winter. Compositional analysis including four height categories of vegetation revealed the following results at the 'location vs. home-range' level (Fig. 4.): In summer we did not observe significant differences in the relative use of the height

int. crops: intermediate crops. >>> denotes a significant deviation, > a non-significant deviation from proportionality at $P < 0.05$. Significant preferences are marked in bold.

Rank orders										Periods
6		7		8		9		10		
grassland	>	bare fields								spring
root crops	>	rape	>	maize	>	**hedges**				summer
tracks	>	cereals	>	root crops	>	bare fields	>	**hedges**		late summer
root crops	>	int. crops	>	grassland	>	bare fields	>	**hedges**		autumn
bare fields	>	tracks	>	cereals	>	grassland				winter

categories ($\lambda = 0.71$, $P = 0.42$, $n = 1888$ locations from 11 pairs). During winter, however, the birds' habitat use was significantly biased towards areas with high vegetation ($\lambda = 0.012$, $P = 0.05$, $n = 800$ locations from 5 coveys). The resulting ranking according to relative use was "less than 0.1 m" <<< "0.1 to 0.5 m" <<< "0.5 to 1.0 m" <<< "over 1.0 m" (<<< indicating a significant difference at $P<0.05$). On average, 20% ± 6.6 (S.D.) of the locations were recorded in vegetation higher than 0.5m although its coverage was only 4.5% ± 0.9. This indicates a strong preference for vegetation that provides cover.

Allocation of time among vegetation types

The log-ratios used in compositional analysis give an estimate of the relative proportion of locations in a habitat structure compared to its availability, thus indicating preference or avoidance of habitat types. However, a structure that is highly preferred in terms of relative use, may nevertheless share only a relatively small proportion of the total of locations, indicating that considerable proportions of activity time may be allocated to non-preferred structures. This was obviously true for the Grey Partridges which, despite their strongly over-proportional use of hedges and wild-flower strips, spent a large proportion of time in cultivated fields (Fig. 3 a,b). In summer, frequently visited vegetation types were cereals (average 26.1% of locations), root crops (14.8%) and grassland (9.3%). In winter, the birds spent much of their activity in cereals or stubble fields (32.7%) and rape (24.1%). This indicates that these types of vegetation, particularly cereals, were attractive resources, although not preferred in respect to their availability.

The density of locations decreased strongly with the distance from wild-flower strips and hedges (Figs 2, 5a). Figure 5b shows the average kernel density in relation to the distance

from the next enhanced area. This response curve indicates that the density of locations declined strongly with distance from ecologically enhanced areas. Location densities within these plots were high, however the maximum average density was re-corded at a distance of 40 m. The distribution corresponds strikingly well to a *Chi²* distribution ($r^2_{adj.} = 0.98$, $n = 20$ class avgs, $P < 0.0001$, Fig. 5b). 65% of all locations were therefore recorded within less than 100m from the next wild-flower strip or hedge. The example given in Fig. 5a illustrates with one family group that the partridges' home range use was indeed mainly determined by the two wild-flower strips available within their home-range.

The standards for the contracts with farmers resulted in a rather uniform distribution of the size of enhanced areas, with only three larger areas where entire fields were converted into ecologically enhanced areas. Consequently, we could not test for eventual effects of the size of ecologically enhanced areas on the partridges' range use.

Fig. 3. The relative availability of 12 vegetation categories and the use of these by Grey Partridges in relation to five time periods. Sample sizes are given in Table 1. a) crop habitats, b) permanent vegetation types. t = proportions available in the study area, h = proportions within home-ranges, l = proportions in radio-location data.
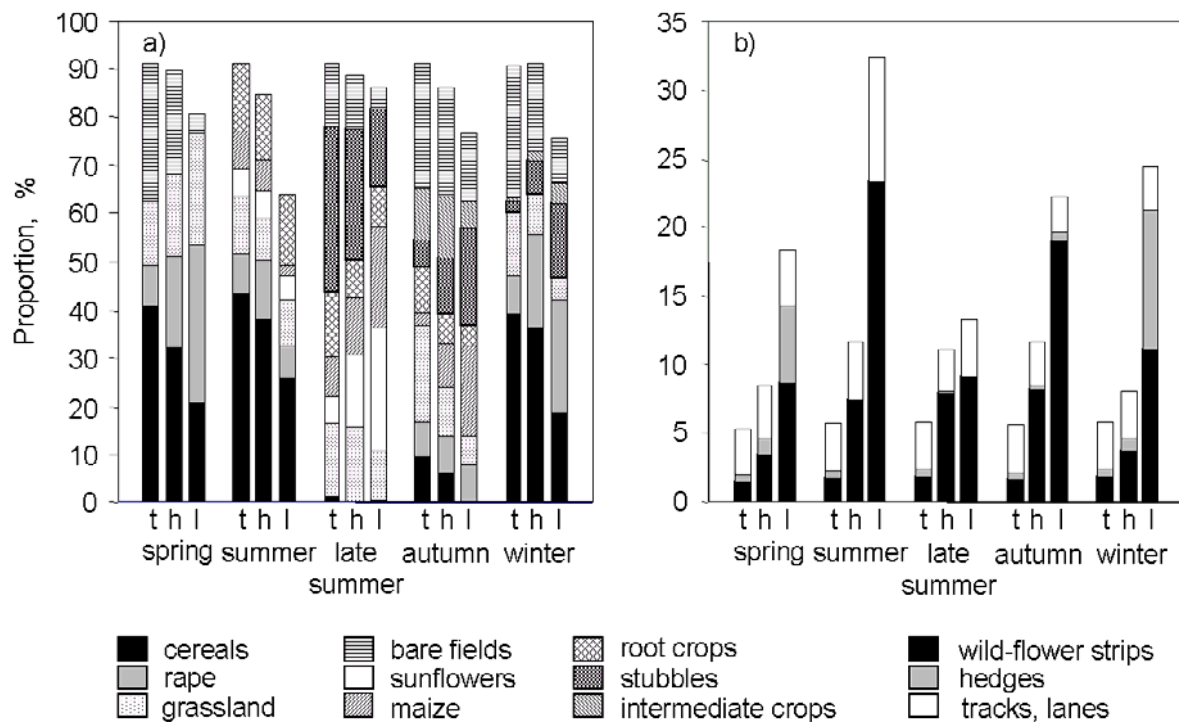
Fig. 4. The range use of Grey Partridges in relation to vegetation height in 1998 - 2000. a) Vegetation period, n = 11 pairs, 1888 locations. b) Winter, n = 5 family groups, 800 locations.
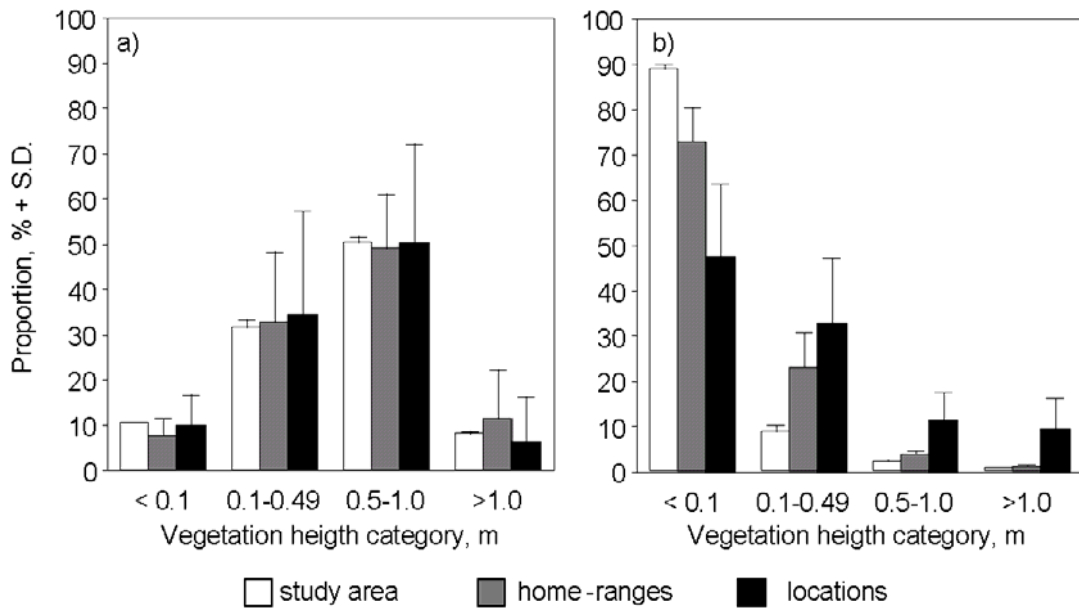
Fig. 5a. Example of the home-range of a breeding pair in the summer period of 1998 (1.5.-31.7., n = 203 radio-locations) illustrating the distribution of locations in relation to the two wild-flower strips available in their home-range. Shaded areas = wild-flower strips, circle = nest site, black dots = locations obtained during egg laying and nesting, grey dots = locations obtained after hatching, field no. 1 = sugar beet, no. 2 = extensively managed summer cereal , no. 3 & 4 = winter wheat.

Fig. 5b. Response curve giving the relative density of all partridge locations in relation to the distance from the next ecologically enhanced area. Averages (± S.E.) over 20 distance categories were calculated for all grid intersections (20x20 m) with kernel densities >0.
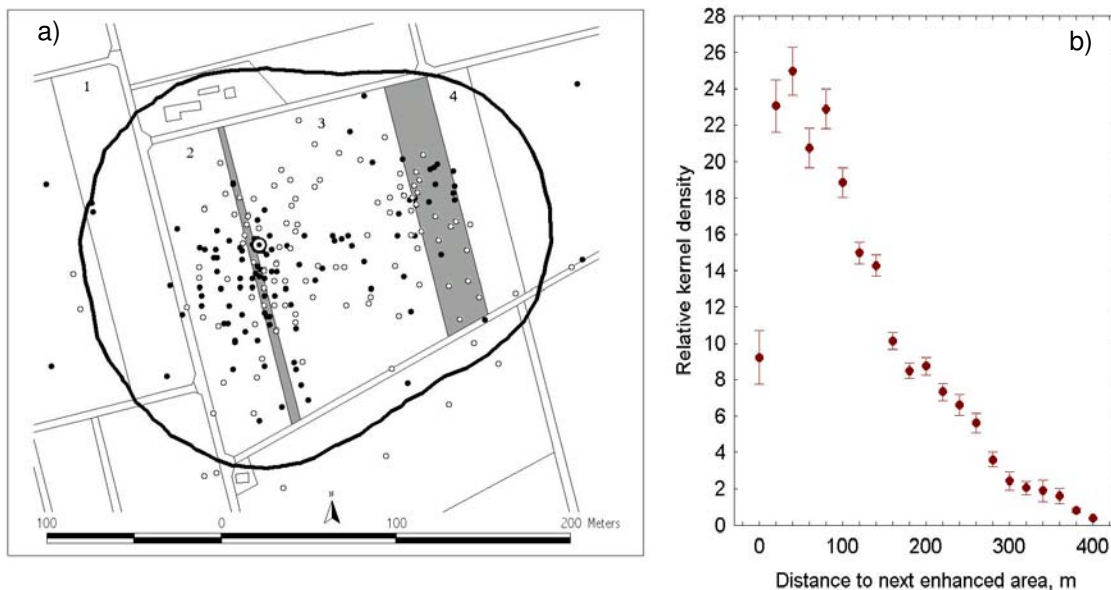
DISCUSSION

Within the study area, the released partridges preferred the parts with the highest density of ecologically enhanced areas. Also, the birds' range use within their home-ranges was mainly determined by the availability and spatial distribution of enhanced areas. The partridges spent most of the time within or very close to these areas. Depending on the season, 9 to 23% of all locations were recorded in wild-flower strips and hedges, although these covered only 2.6% of the study area. In total, 65% of all locations were recorded within less than 100 m from ecologically enhanced areas. This concentration was particularly strong during chick-rearing, when protein food is required (e.g. Southwood & Cross 2002), and in winter, when adult predation rates are high (e.g. Pegel 1987).

Compared to other studies, the chick survival did not differ from the survival rates reported from wild partridge populations (e.g. Potts & Aebischer 1995, Putaala & Hissa 1998, Bro *et al*. 2000a; a detailed analysis will be published separately, *see Chapter III*). We conclude from this that providing a mosaic of wild-flower strips and hedges (although small in proportion) was the crucial ecological improvement that restored the area to allow the released birds to survive and reproduce, which was a successful first step towards re-introduction. However, as data on long-term survival and reproduction are not yet available, our analyses do not allow conclusions to be drawn on the long-term sustainability of the new small population. Also, estimating the potential capacity of the habitat for a larger population is not possible. During the study, the density of partridges in the study area was very low (1.5 pairs/100 ha, compared to the 10-80 pairs/100 ha reported by e.g. Jenkins 1961, Birkan *et al*. 1992).

Although wild-flower strips and hedges were highly preferred habitat structures, a large proportion of the birds' activity was spent in other vegetation types, including agricultural fields, which were used in an opportunistic way, i.e. proportional to the availability in the respective home-ranges. However, the partridges stayed close to wild-flower strips and hedges while exploiting any other resource (Fig. 5). Therefore, the particular pattern in the partridges' range use resulted from the combination of both effects, the significantly over-proportional use of wild-flower strips and hedges, and the significant decrease in location density with distance from these when using any other vegetation category. We believe that this pattern in the habitat and range use is primarily related to predator avoidance. Partridge predation rates are naturally high throughout the year and therefore, the availability of cover is a key factor for partridge survival (Potts 1986, Pegel 1987, Aebischer 1997).

Besides the preference for the permanently available enhanced areas, the birds used the arable cultures according to their availability. Much of their activity was spent outside ecological enhancements, for example in cereal crops. This indicates that the arable fields offered important resources, presumably food, and thus were also an important part of their habitat (Green 1984, Carroll *et al.* 1995, Bro *et al.* 2000c).

In general, the home-range areas were similar to those reported from short-term studies (Schulz 1980, Birkan *et al.* 1992, Carroll *et al.* 1995). In addition, our data demonstrate a marked seasonal variation of home-range size. During spring and summer, home-ranges were about half the size (*avg.* 6.9 ha) of that during late summer, autumn and winter (*avg.* 15 ha), probably related to changes in the social organisation of the partridge. The spring and summer home-ranges were occupied by breeding pairs only, whereas during the rest of the year they were occupied by partridge family groups (coveys) which stay together until late winter or early spring.

Conservation implications

Our results emphasise the importance of uncultivated structures and non-crop areas to the biodiversity in agricultural landscapes (Freemark & Kirk 2001). The released Grey Partridges strongly preferred the part of the study area with the highest density of ecologically enhanced areas. These newly established habitat structures were the main determinants of the birds' range use within the home-range. They were the cores in the home-ranges, from which the birds exploited the surrounding agricultural fields. We therefore suggest that intensively cultivated arable areas should be prepared for re-colonisation by partridges by providing (treeless) hedges (Rands 1987), permanent wild-flower strips and/or other perennial vegetation. A web of many small but ecologically valuable areas appears to be appropriate for providing the habitat structure that allows partridges to survive and to reproduce. In the most preferred part of the study area, the proportion of enhanced areas was 5.8%. Thus, establishing a mosaic of ecologically enhanced areas is the first-rate measure of preparing the re-introduction of this species.

Acknowledgements

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Effects of human and predator disturbance on Grey Partridge *Perdix perdix* behaviour

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Abstract

Disturbance has been shown to have short-term impacts, by inducing changes in behavioural responses, as well as long-term impacts by provoking spatial shifts in distribution. To quantify the disturbance potential of human and predator disturbance on free-living Grey Partridges *Perdix perdix* in the Swiss Klettgau we analysed the behavioural responses of this species towards sources of human disturbance such as leisure activities, farming activities and traffic, as well as predator disturbance caused by raptors and mammals during daytime. Partridges showed a distinctive cause-specific reaction repertoire to all different disturbance types, mainly crouching in presence of raptors and vigilance in presence of mammals. Flushing was the main reaction when disturbed by leisure activities. When forced to fly, partridges reduced their flight distance by 54 metres compared to unforced flights and remained in their territory in 87% of all cases. The spatial distribution of partridges was influenced by season: In summer, partridges avoided areas with high human disturbance whereas in winter they avoided areas with high predator abundance and close proximity to tall hedges. Human activities caused twice as much disturbance events as predators, with associated energetic costs. Overall, disturbance substantially limited the partridges' spatial use, with consequences for the carrying capacity of the area.

INTRODUCTION

As a result of the increase in human population, its mobility and leisure time, human pressure on natural and semi-natural areas has been growing exponentially. The question of whether and to what extent human presence has adverse effects on wildlife has therefore become a major concern of conservationists in recent years (Hockin *et al.* 1992, Hill *et al.* 1997). Assessing the severity of the effects of human presence has also important practical consequences; if the impact is serious, conservationists are justified in recommending restrictions for the access to wildlife areas (Tuite *et al.* 1984, Beale & Monaghan 2004).

Most studies on the effect of disturbance relate to coastal areas, many being focused on waterfowl and shorebirds *(Anseriformes* and *Charadriiformes)* because these birds frequently occur on areas with high levels of human disturbance (Kirby *et al.* 1993, Carney & Sydeman 1999) and are, compared to most other bird groups, relatively easy to observe. Comparatively few studies have focused on farmland birds, even though these species live in a long human-

disturbed environment and many are of European conservation concern (Tucker & Heath 1994).

One of those species is the Grey Partridge *Perdix perdix*. The main reasons for its dramatic decline (Aebischer & Kavanagh 1997) have been identified as the effects of intensive farming practices and increased predator numbers (e.g. Potts 1986). Partridges are prey to a wide range of different predator species which have long been implicated as a major selective force in the evolution of behavioural characteristics of animals (e.g. Lima & Dill 1990). On the other hand, partridges have been exposed to human disturbance – mainly farming and shooting - for centuries. We might therefore expect that anti-predator behaviour strategies have evolved along with specific behaviour to keep the costs of human disturbance as low as possible. Despite this, an increase in human disturbance might well have damaging effects. There is growing evidence that human presence can prevent successful breeding (Schulz & Stock 1993; Giese 1996, Beale & Monaghan 2004) or increase mortality rates (e.g. Wauters *et al.* 1997, Watson & Moss 2004), for a literature review see Keller (1995). However, in many cases disturbance may act in a more subtle way, by reducing access to resources such as food supplies or nesting sites (Gill 1996; Gill *et al.* 2001). Gill *et al.* (1996) have shown that, on a local scale, the impact of disturbance can be viewed as a trade-off with resource use in the same way as minimizing predation risk has been shown to impede optimal habitat selection and use (Werner *et al.* 1983, Milinski 1985, L'Abée-Lund *et al.* 1993).

This study examines 1) how wild living partridges react to different types of disturbance, 2) whether forced flights have an impact on distance moved, 3) which habitats partridges use as escape cover, and 4) how the spatial distribution of humans and predators influences the spatial distribution of partridges.

STUDY SITE

This study was conducted in part (530 ha) of the Klettgau, an intensively used arable region near Schaffhausen, Switzerland (430 m a.s.l.). Since 1991, the Klettgau has been subject to ecological enhancements, particularly by promoting sown and spontaneous wild-flower strips, which have been shown to be valuable landscape structures for partridges (Buner *et al.* 2005). Besides agricultural use (for more details see Buner *et al.* 2005), the study area is very popular for recreation mainly by walkers with or without dogs and riders. In the centre of the study site there is a dog training school and an arena to school horses, in the northern part of the area there is a cycling route.

METHODS

Data collection

As this study is part of a partridge re-introduction evaluation project that has been conducted from 1998 to 2000, all partridges used for this study have been either released or are direct offspring of released birds[1]. The collection of the data used in this analysis started one month after release and continued as long as at least one radio-transmitter per pair or family group (i.e. covey) was working, or until single birds lost their transmitter. Each sample unit (i.e. pair, covey or single bird) was located 1-4 times daily (the period between leaving and settling at the roost site), depending on the number of birds under observation, with a minimum of one hour between two consecutive sessions with the same group. Each unit was also observed during a continuous one-hour period in 5-minute intervals (12 observations per hour) at least once a week. All observation sessions were distributed randomly over daytime. No data was collected at the birds' roost sites. For every observation we noted the birds' location and behaviour as well as the cover habitat to which the birds flew after they had taken flight. If the birds under observation were disturbed, we additionally noted the source of the disturbance and the ensuing behavioural response. To analyse the disturbance rate, only the data from the continuous one-hour observations were used. To determine the behavioural responses to the different disturbance types and flight distances, the data from the continuous as well as the daily observations were used. Owing to the fact that partridges are normally not disturbed when observed from a vehicle, the continuous observations were always made from a car. The few disturbance events that were caused by the observer were excluded from the analyses.

Disturbance categories

Disturbance was divided into two main categories, human disturbance and predator disturbance. A) Human disturbance was divided into three main categories. 1) Leisure activities: This included all walkers with or without dogs as well as riders, who were sometimes accompanied by dogs too. 2) Farming activities: All sowing, ploughing and harvesting activities with machinery as well as farmers walking around inspecting their fields or doing work by hand. 3) Traffic: All cars and bicycles passing through the study site, except

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[1] For detailed descriptions of the origin and number of birds released, releasing techniques, transmitters used, catching techniques, habitat use and survival see Buner *et al.* 2005 and Buner & Schaub 2008, *or see Chapters III & IV in this Volume.*

the vehicle of the observer. B) Predator disturbance was divided into two main categories. 1) Raptors*: All birds of prey that regularly occurred in the study area such as Common Buzzards *Buteo buteo*, Hen Harriers *Circus cyaneus*, Red Kites *Milvus milvus*, Kestrels *Falco tinnunculus* and Sparrowhawks *Accipiter nisus*. 2) Mammals: Domestic cats *Felis catus* and Foxes *Vulpes vulpes*.

Partridge behaviour

The behavioural patterns of Grey Partridges in response to human and predator disturbance were divided into five main types. 1) Vigilance: A neck stretch involving a complete raising of the body to an upright stance, or flicking the tail and making jerky movements without any greater displacement. 2) Crouch: A rapid squatting of the bird into a hunched position, whereby it would attempt to flatten itself against the ground. 3) Run away: Running away for just a few metres, but always remaining in the same type of habitat as the one in which the bird was disturbed. 4) Run/flee into cover: Running to adjacent cover (mostly a different habitat type from the one in which the bird was disturbed), with head and neck partly outstretched and held lower than the line of the body. 5) Flush: taking off with great acceleration, then gliding low over the ground with occasional wing beats to reach cover at greater distance. 6) Defence: Observed in 15 cases when adult partridges successfully defended themselves and their juveniles against attacking Kestrels, by jumping towards the attacker, using their beak to drive away the bird of prey. This behaviour was never observed as a reaction to human disturbance, and was therefore excluded from further analysis.

Monitoring of human activities and predator abundance

The level and spatial distribution of human activities in the study area was monitored during 1999 and 2000. Each weekday was monitored once in each month of the sampling period and when weather conditions were dry. Every observation session lasted for one hour and took place between 16.00 and 18.00 when the probability of observing all human activities was highest. The three different categories defined were 1) leisure activities, 2) farming activities and 3) traffic (see also section 'Disturbance categories'). The precise location of all humans present was noted in five-minute intervals on a 1:5000 map, and later digitised using Arc View GIS 3.2. A small hill in the northern part of the study site, from which approximately 90% of the whole study area could be surveyed, served as the observation point.

Mammalian predators (foxes and cats) were counted during two consecutive dry nights each month between 1998 and 2000 using a car, binoculars and two spot-lamps (Heydon et al. 2000). Although our analyses examine the impact of disturbance on the spatial distribution of partridges during daytime, we believe that the assessment of the spatial distribution of foxes and cats during night-time only, poses no conflict to our analyses. First, because it has been shown that the range sizes of cats and foxes do not differ between day and night (Molsher 1999, Reynolds pers. comm.), and second because Grey Partridges do roost within their foraging area. Even if Grey Partridges are mainly disturbed by those two predators during the night (foxes are mainly night active, Reynolds & Tapper 1995) an avoidance will therefore be mirrored in the partridges' daytime spatial use as well. The counts were carried out along a defined route, which ensured a maximum coverage of the study area from east to west or vice versa. The starting and finishing points of the census were altered between consecutive counts. The travel speed was approximately 20 km/h, the duration of the whole count approximately 2.5 hours and recording was carried out between 20.00 and midnight.

Raptors were counted on two different days at the end of each month between 1999 and 2000 using a car and binoculars. The counts were carried out along a defined route during mid-morning or late afternoon, ensuring a maximum coverage of the study area. The duration of the counts took one hour.

All raptor and mammal locations were noted on a 1:5000 map and later digitised using Arc View GIS 3.2.

Analyses

Causes of disturbance

To assess whether the relative importance of each of the three human activity types (traffic, farming and leisure) differed between the two seasons summer (May-July) and winter (November-February) we used compositional analysis (Aitchison 1986). We used the observation day (n = 21 in summer, n = 28 in winter) as the unit for analysis, calculated the proportion of each activity type on each observation day, transformed the three daily proportions to two logratios (using traffic as denominator), then compared the mean summer and winter logratios by MANOVA, testing for equality using Wilk's lambda.

Effects of disturbance on flight distances

Flight distances were calculated measuring the distance between observed take-off location

and landing location, using Arc View GIS 3.2. The following two measures were used to quantify the costs of additional flights: 1) landing location inside or outside the home-range boundary of the group observed, 2) distance between take-off and landing location. The home-range boundary was calculated using fixed kernel estimation (Spatial Analyst tool, Arc View GIS 3.2, cell size 20 m, radius 50 m) and the contour covering 95 % of the density distribution was denoted as the home-range area (for more details see Buner *et al.* 2005).

Effects of disturbance on spatial distribution

To analyse the influence of human activity and predator distribution on the partridges' spatial distribution, we calculated the spatial ranges of the human activities and predator groups using fixed kernel estimation (Spatial Analyst Tool, ArcView GIS 3.2, cell size 10 m, radius 100 m for all human activities combined and 350 m for the three predator groups raptors, foxes and cats separately) and denoted the contour covering 80 % of the density distribution as the area with high disturbance level, and the area outside that contour as the area with low disturbance level. The GIS analysis of fox data revealed a uniform distribution pattern over the whole study area, which meant that partridges could not choose between areas of high or low fox abundance, we therefore excluded the fox data from further analyses. Gill *et al.* (1996) showed that the effect of disturbance can be viewed as a trade-off between efficient use of resources and predator avoidance. Buner *et al.* (2005) found that the key resources of partridges in this study were wild-flower strips during summer and hedges during winter, and that partridges preferentially stayed within around 100 m of the nearest enhanced area (i.e. a wild-flower strip or hedge). The mean flight distance of partridges after disturbance was 140 m (see Results), so an essential resource (wild-flower strips in summer and hedges in winter) can be optimally used only as long as the birds remain within 140 m of these resources. We therefore calculated a buffer of 140 m around wild-flower strips in summer and hedges in winter using Spatial Analyst Tool, ArcView GIS 3.2., and defined those areas as the zones of high resource value for partridges. The areas lying outside those buffers were defined as being of low resource value (Fig 1). To assess whether the spatial distributions of partridge pairs in summer (May-July) and coveys in winter (November-February) were random with respect to the level of each type of disturbance (human or predator), we used the pair/covey as the basic unit for analysis (n = 11 pairs in summer, n = 5 coveys in winter). For each pair/covey, we calculated the proportion of radiolocations in areas of high disturbance using ArcView GIS 3.2. After logit transformation, we compared the average across pairs/coveys with the logit of

the proportion of the study area subject to high disturbance using a t – test (assessing the level of significance by randomisation to avoid any effect of non-normality).

Additionally we assessed the effect of hedge structure (classifying hedges into ones with/without trees) on the spatial distribution of partridge coveys in winter. For each covey, we calculated the observed proportion of covey locations within 140 m of the nearest hedge type, transformed the proportions to logits and compared the average with the logit of the proportional availability in the study area using a t – test (assessing the level of significance by randomisation).

RESULTS

Rates and causes of disturbance

We observed 25 different Grey Partridge units (i.e. single birds, pairs or coveys) on 497 days and 1163 continuous one-hour observations, which provided 13,961 records. Of those, 240 (1.7%) records were behavioural responses to human disturbance events and 291 (2.1%) were caused by predators.

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Among all human disturbance events, leisure activities were the most common cause of disturbance (53.8%, n = 129), followed by farming activities (23.7%, n = 57) and traffic (22.5%, n = 54). Among all recorded diurnal predator disturbance events, raptors were responsible in 79.0% of all observed cases (n = 230, of which buzzards 105, kestrels 39, harriers 46, kites 36 and sparrowhawks 4), and mammals in 21.0% of cases (n = 61, of which cats 51 and foxes 10). Over the year most disturbance events were recorded in winter (Tab 1).

The rate of disturbance by human activities did not vary between summer (*avg.* = 0.11, *SD* = 0.08) and winter (*avg.* = 0.08, *SD* = 0.06), indicating that overall human disturbance levels were the same during the two periods (U = 40, P = 0.3, Mann-Whitney test). However, the relative importance of each of the three human activity types was significantly different between the two seasons (Λ = 0.52, P < 0.0001, MANOVA). The relative level of leisure activities was much higher in winter (mean = 44%) than in summer (29%), whereas the level of farming activities was higher in summer (41%) than in winter (33%).

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Table 1. Number and proportion of recorded causes of diurnal disturbance of wild living Grey Partridges (n = 25) to human and predator disturbance events over the year (Spring = March-April, Summer = June-July, Autumn = September-October, Winter = November-February).

Cause	Spring		Summer		Autumn		Winter		Overall	
	n	*(%)*	n	*(%)*	n	*(%)*	n	*(%)*	n	*(%)*
Leisure	16	*(6.6)*	21	*(8.8)*	33	*(13.8)*	59	*(24.6)*	129	*(53.8)*
Farming	7	*(2.9)*	9	*(3.8)*	31	*(12.9)*	10	*(4.2)*	57	*(23.8)*
Traffic	7	*(2.9)*	7	*(2.9)*	20	*(8.3)*	20	*(8.3)*	54	*(22.4)*
Raptor	25	*(8.6)*	23	*(7.9)*	44	*(15.1)*	138	*(47.4)*	230	*(79.0)*
Mammal	7	*(2.4)*	11	*(3.8)*	26	*(8.9)*	17	*(5.8)*	61	*(21.0)*
Overall	62	*(11.7)*	71	*(13.4)*	154	*(29.0)*	244	*(45.9)*	531	*(100)*

The rate of disturbance by partridge predators (mammals and raptors together) did also not differ between the two seasons ($U = 158.5$; $P > 0.05$, Mann-Whitney test). However, the number of mammalian predators was significantly higher during summer (n = 23 nights, *mean* = 21.4 individuals / 6 km^2, *SD* = 8.4), than during winter (n = 33, *mean* = 16.8, *SD* = 4.7, $U = 239$; $P < 0.05$). Conversely, raptor numbers on the other hand, were significantly lower in summer (n = 14 days, *mean* = 11.4 individuals / 6 km^2, *SD* = 3.0) than in winter (n = 27, *mean* = 19.4, *SD* = 9.2, $U = 61$; $P < 0.05$, Mann-Whitney test).

Behavioural responses

When disturbed by humans, the main reaction of partridges was 'flush' (28.8%, n = 69), followed by 'crouch' (22.1%, n = 53), 'vigilance' (19.6%, n = 47), 'run away' (15.4%, n = 37) and 'run/flee into cover' (14.2%, n = 34), $Chi^2 = 16.3$, df = 4, $P < 0.002$. Leisure activities were responsible for the majority (76.8%, n = 53) of all 69 observed flushes caused by humans, whereas traffic caused 14.5% (n = 10) and farming activities only 8.7% (n = 6), Chi^2

= 59.03, df = 2, *P* < 0.01. When disturbed by predators, the reaction pattern of the Grey Partridges was very different from human disturbance (Chi^2 = 121.9, df = 4, *P* < 0.001). 'Crouch' (55.0%, n = 160) was the most frequently performed reaction to predator disturbance, followed by 'vigilance' (27.5%, n = 80), 'flush' (9.3%, n = 27), 'run/flee into cover' (7.5%, n = 22) and 'run away' (0.7%, n = 2). Between the two predator groups, there were remarkable differences (Chi^2 = 67.1, df = 4, *P* < 0.001). When disturbed by raptors, the main response was 'crouch' (63.2%, n = 153), whereas the main response to mammals was 'vigilance' (57.1%, n = 28), see Table 2. In conclusion: The most energetic reaction type 'flush' was more than twice as frequent in behavioural responses caused by human disturbance (0.49% of all 13,961 recordings) than in those caused by predators (0.19%) and was mainly caused by leisure activities.

Table 2. Number and proportion of recorded behavioural responses of wild living Grey Partridges (n = 25) to human and predator disturbance events during daytime.

Cause	Flush		Crouch		Vigilance		Run away		Run into cover	
	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)
Total human (n = 240)	69	(28.8)	53	(22.1)	47	(19.6)	37	(15.4)	34	(14.2)
Leisure	53	(41.1)	31	(24.1)	15	(11.6)	15	(11.6)	15	(11.6)
Traffic	10	(18.5)	15	(27.8)	14	(25.9)	8	(14.8)	7	(13.0)
Farming	6	(10.5)	7	(12.3)	18	(31.6)	14	(24.6)	12	(21.0)
Total predator (n = 291)	27	(9.3)	160	(55.0)	80	(27.5)	2	(0.7)	22	(7.5)
Raptors	15	(6.2)	153	(63.2)	52	(21.5)	0	(0.0)	22	(9.1)
Mammals	12	(24.5)	7	(14.3)	28	(57.1)	2	(4.1)	0	(0.0)

Flight distances

There was no difference (*U* = 1160, *P* = 0.78, Mann-Whitney test) between the mean flight distances after predator disturbance (n = 34) and human disturbance (n = 80). The data were therefore pooled. There was, however, a significant difference (*U* = 4141.5, *P* < 0.001, Mann-Whitney test) between the mean flight distances of all disturbed birds (*avg.* = 137 m, *SD* = 86 m, n = 114) and the flight distances of birds flying undisturbed to their roost sites (*avg.* = 191 m, *SD* = 109 m, n = 103).

For 70 'flush' disturbance events (41 human-, 29 predator disturbance events) for which the territory boundary of the sample unit (n = 15) was known, only 9 cases (7 human-, 2 predator disturbance events) revealed landing locations beyond the territory boundary.

However, for all cases where partridges left their territory owing to human disturbance, leisure activities were the cause. All birds that left their territory owing to disturbance had returned by at least the next day.

Escape cover

The escape cover type used by partridges differed between the seasons. During the summer period (May-July, n = 43), partridges flew into cultivated habitats in 79% of all cases and into permanent structures (i.e. wild-flower strips) in 21%. During the winter period (November-February, n = 50) 50% of the escape cover habitats were permanent structures (34% hedges and 16% wild-flower strips) and 50% cultivated habitats, indicating that permanent structures are much more important as escape cover during winter than in summer. Furthermore partridges made greater use of areas with small treeless hedges than areas with hedges with trees than expected from availability ($t = 2.66$, $P = 0.05$).

Spatial distribution

In summer the proportion of partridge locations (n = 11 pairs, *avg.* = 151 locations per pair) in areas of low and high human disturbance differed significantly from the proportions available within the study area, indicating that partridges avoided areas of high human disturbance ($t = 2.25$, $P = 0.05$). No influence ($t = 0.04$, $P = 0.98$) on spatial distribution was found by predator distribution (i.e. raptors and cats together), indicating that partridges used their preferred resources unaffected by predators during summer. In winter on the other hand, partridge distribution (n = 5 coveys, *avg.* = 156 locations per covey) was affected by predator distribution ($t = 12.98$, $P = 0.05$). The partridges were significantly less often located in areas affected by high predator abundance, while human disturbed areas did not seem to influence spatial distribution ($t = 0.47$, $P = 0.67$), indicating that in winter partridges tolerated human disturbance more than during summer.

DISCUSSION

Grey Partridges possess a distinctive cause-specific repertoire of behavioural reactions. When disturbed by raptors, partridges mainly crouched, whereas when disturbed by diurnal mammalian predators they mainly remained vigilant. As a typical ground-living bird, the Grey Partridge flies only occasionally, mainly during dawn and dusk when leaving or flying

into the roost site, which presumably is a behaviour to avoid predators (Jenkins 1961, Dowell 1990). Additional flights during daytime are likely to pose a threat to the birds because they increase their visibility to predators. In the presence of a predator, 'flush' is therefore probably not a viable behaviour, whereas crouching in the presence of a raptor normally ensures that the raptor passes its prey unnoticed (pers. observation). 'Vigilance' on the other hand, seemed to be the behaviour with the best cost/benefit ratio when birds were approached by a mammal, probably because mammals usually give up hunting when they have been recognised by their prey (pers. observation).

Fig. 1. Spatial distribution of partridges (black dots = pooled sample of all partridge locations, n = 5 coveys) and areas subjected to different categories of disturbance in the study area during winter. Black outlines endorse areas of high nocturnal cat density, black hatched outlines endorse areas of high raptor density, grey shaded areas denote areas of high human activity.
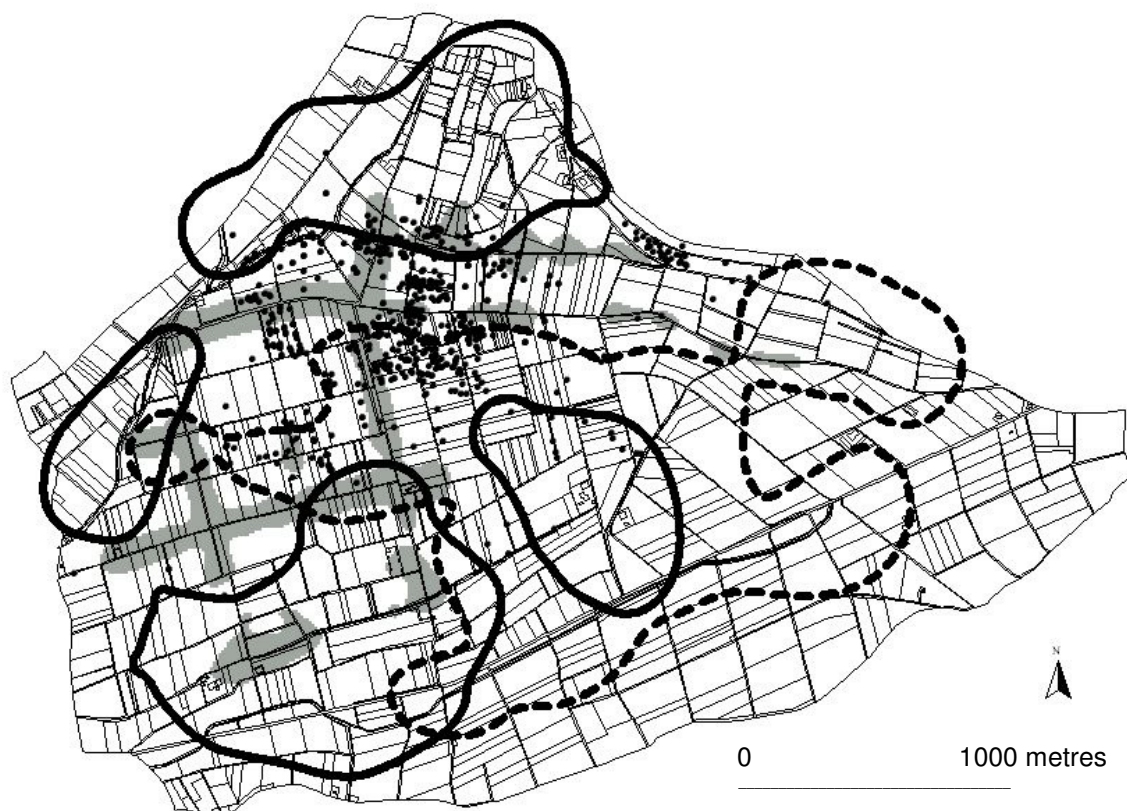
In contrast, when disturbed by humans, 'flush' was more than twice as frequent as when disturbed by predators. Human activities caused 71.8% of all observed flushes (n = 96), leisure activities alone 41.1% and walkers with their dogs accounted for the majority of these (55.2%). Walkers, especially when accompanied by dogs, are widely believed to have

disturbance impacts on ground-nesting birds, lowering breeding success in the worst case (Berlich & Müller 1994, Eislöffel 1996). This effect could not be tested during this study owing to the low number of nesting birds (see Buner & Schaub, submitted). However, disturbance may also have more subtle impacts such as energetic costs. Disturbed partridges minimized their flight costs by significantly shortening their flight distance, compared to undisturbed flights. They also remained within their home- range area in the majority of cases (87%). Farming activities on the other hand, historically the main cause of disturbance in arable landscapes, disturbed partridges only half as often as leisure activities.

Farmland birds are generally not considered to show strong avoidance of humans (Tucker & Heath 1994), whereas predator abundance has an influence on the spatial distribution in several species (Werner *et al.* 1983, Milinski 1985, L'Abée-Lund *et al.* 1993). Gill *et al.* (1996) further showed that, on a local scale, the impact of human disturbance can also be viewed as a trade-off with resource use.

Combining the trade-off between predator and human disturbance and resource use reveals a particular result in the case of the Grey Partridge. During the breeding season, areas of high human disturbance were avoided, whereas in winter avoidance was less pronounced. This suggests that human disturbance might have had a negative impact on the breeding performance of the released partridge population. Predators (cats and raptors), on the other hand, were avoided in winter and more tolerated in summer, presumably because the overall cover supply in summer was much better than in winter. Avoiding areas with high predator abundance meant that large parts of the study area were left unused in winter (see Fig. 1), despite the fact that the winter food of partridges (mainly cereal grains and green leaves; Middleton & Chitty 1937, Potts 1986) must have been widely distributed over the study area. Furthermore, the fact that areas containing hedges with trees were significantly less used than expected, indicates that they were not optimal for foraging, although hedges and their surroundings were the most used habitat type relative to availability in winter (Buner *et al.* 2005) and also one of the most used escape covers. Hedges with trees as well as woodland edges are ideal for perching raptors (Newton 1979) and foraging near such sites would be risky for partridges (e.g. Dudzinski 1992). It seems therefore that in winter, avoiding areas with the highest predation threat was more important than avoiding areas of high human disturbance.

In this study, humans caused twice as many disturbance events as predators, especially additional flights, which are likely to increase energy costs and contribute to breeding failure.

High predator abundance in combination with human disturbance may therefore have a severe impact on the carrying capacity of a particular area for Grey Partridges.

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CONCLUSIONS

Despite the best efforts of Swiss agricultural policy and millions of Swiss Francs spent on enhancing agricultural biodiversity, the Grey Partridge, a key farmland bird species, has shown no sign of recovery to the present day. Indeed, the last truly wild partridge population in Switzerland in the Champagne genevoise became almost extinct during the time of this study (3 birds left in 2004). Much more effort is needed therefore, to save the Grey Partridge which depends on high quality habitat enhancement in the right places and in substantial proportion of the available habitat supply (for more details see chapter 4). To save species like the Grey Partridge, carefully planned projects which bring together various stakeholders such as farmers, population biologists, conservationists, game keepers, people from the local, regional and national government, local nature conservation groups and the press are necessary.

This study shows that with enough staying power, even the intensively exploited Swiss countryside may provide a suitable environment for highly demanding species such as the Grey Partridge. Although it is not possible to prove from this study's results whether further partridge re-introductions in Switzerland or abroad will be successful in terms of creating self-sustainable populations (to do so, long term experiments are necessary) it is possible to draw three basic conclusions for Grey Partridge re-introduction projects:

1) Prior to every partridge re-introduction or re-establishment project the habitat must be enhanced with permanent habitat structures. Wild-flower strips and low, if possible treeless hedges are highly preferred by partridges as they provide nesting, brood rearing, foraging and escape cover during all seasons.

2) If translocated wild birds are not available, the most efficient releasing technique is fostering chicks to pairs which failed to hatch their own young. In the best case, chicks are fostered to wild birds still resident in the area. Where no such birds are left, captive parent-reared adults should be released as coveys in autumn with maximum support to allow successful settlement, followed by fostering chicks the following summer. Giving the system enough time to develop, a carefully planned releasing regime should allow a population of well experienced individuals to establish in a relatively short time.

3) To enhance the chances of re-introduction success, areas should be chosen with low predator numbers and human activities, especially leisure activities, or managed specific-ally to reduce those sources of disturbance. Predators and human activities do not only have direct impacts on survival and breeding success but may also reduce the available area for foraging and therefore the carrying capacity of an area as a whole.

4) Sustained post-release monitoring should check for winter mortality, nesting success and chick survival over time. At least one spring and autumn count should be carried out to assess population development of the released birds. In order to find possible weaknesses in a re-introduction project, knowledge of the most important population parameters are essential in order to ensure the project targets are met.

POPULATION PARAMETERS IN THE KLETTGAU 1998-2005

In 2002, the Government of the Kanton Schaffhausen agreed to participate in a re-introduction project under the management of the Swiss Ornithological Institute, based on the findings of this preliminary study. In spring of the same year, 57 wild translocated birds from Poland were released to support the three remaining wild coveys produced by the established birds from this study. From 0 pairs in 1997, the population peaked at 24 pairs in 2002 (when the birds from Poland were released), before falling back to 18 pairs in 2005. The increasing proportion of adult summer survival from 22% in 1998 to 64% in 2005 is the most encouraging result during that period (see table below). It clearly indicates that the birds are increasingly adapting to the environmental factors relevant in the Klettgau. However, although important population parameters such as avg. clutch size, hatching rate and chick survival are well within the levels of natural populations (see this volume), nesting success between 2001 and 2005 is, with an avg. of 40%, just at the lowest possible level for self-sustainability (Potts 1986). If an increased nesting success of the Grey Partridges in the Klettgau can be achieved – most likely by reducing predator pressure and human disturbance during the breeding season - there is legitimate hope that this unique bird will remain on the list of the Swiss breeding birds into the future.

Number of birds released in the Klettgau and the most relevant population parameters based on monitoring data since partridges were first re-introduced in 1998. Data collected from 2002 onwards by Markus Jenny and his team.

Type	Total number of birds							
	1998	1999	2000	2001	2002	2003	2004	2005
Birds released	10	108	24	0	117	62	59	46
Translocated	100%	21%	-	-	49%	-	-	-
Fostered	-	7%	100%	-	30%	90%	83%	93%
Reared adults	-	72%	-	-	21%	10%	17%	7%
Pairs in May	4	5	9	7	24	?	15	18
Summer survival of adults	22%	30%	35%	31%	?	?	?	64%
Nesting success	25%	0%	22%	43%	46%	?	40%	33%
Family groups in Oct	1	0	2	3	11	7	6	6
Juv./Family in Oct Mean *(SE)*	10.0 *(0.0)*	0	7.5 *(6.5)*	?	?	?	7.6 *(1.1)*	6.2 *(1.2)*

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CURRICULUM VITAE

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Personal Data

Geboren:	10. Februar 1972
Heimat- & Geburtsort	Basel
Nationalität	Schweizer
Zivilstand	Ledig

Education

1978	Eintritt in die Primarschule Lupsingen, BL
1990	Matura Typus M (Musik & Zeichnen) am Gymnasium Liestal
1991-1998	Studium in Biologie I an der Universität Basel

Nebenfach: Natur-, Landschafts- & Umweltschutz, NLU (Prof. Dr. B. Baur & Prof. Dr. H. Leser)

Nebengebiete: 1. Oekologie und Systemökologie der Pflanzen (Prof. Dr. C. Körner); 2. Biologie der Wirbeltiere (Prof. Dr. B. Bruderer); 3. Biologie der Wirbellosen (PD Dr. P. Duelli & PD Dr. C. Weber)

Hauptgebiet: Populationsbiologie, Evolution, Oekologie, Verhaltensökologie (Prof Dr. S.C. Stearns)

1996. Mitarbeit an der Pilotstudie über „The summer ecology and habitat use of the turtle dove" beim Game and Wildlife Conservation Trust, Fordingbridge, UK, unter der Leitung von Dr. N.J. Aebischer.

1997-1998. Diplomarbeit an der Universität Basel unter der Leitung von Prof. Dr. B. Bruderer zum Thema „Habitat use of overwintering Kestrels *Falco tinnunculus* in relation to perch availability, vole abundance and distribution".

1998-2006	Dissertation an der Universität Basel und der Schweizerischen Vogelwarte Sempach unter der Leitung von Prof. Dr. B. Bruderer zum Thema „Survival, habitat use and disturbance behaviour of re-introduced Grey Partridges *Perdrix perdrix* L. in an enhanced arable landscape".
2004-2007	Post-doc Stipendium (Westminster Overseas Research Fellowship) beim Game and Wildlife Conservation Trust, Fordingbridge, UK, über "Determining optimal release methods as a tool for restoring the abundance and range of Grey Partridges in the UK", unter der Leitung von Dr. N.J. Aebischer.

Professional Experience

1985/1986	Praktika im Zoologischen Garten Basel (je 2 Wochen) im Vogelhaus
1989/1990	Mitarbeit (je 1 Woche) auf den Beringungsstationen Portalban, FR und Ulmethöchi, BL
seit 1991	Exkursionsleiter des Schweizer Vogelschutz (SVS)
	Leiter der Jugendgruppe von Pro Natura Baselland
1991	Lancierung des Projektes „Hecken fürs Baselbiet" welches 1992 mit dem Prix Toni ausgezeichnet wurde (dotiert mit sFr. 10,000).
1992	Organisation und Leitung eines 2-wöchigen Naturschutz-Arbeitseinsatzes in der Estremadura (ESP)
1992/1993	Mitarbeit am Ornithologischen Inventar Beider Basel
1993	Teilzeit-Anstellung als Kuratorassistent am Naturhistorischen Museum Basel bei Dr. R. Winkler
1994	Mitarbeit (insgesamt 3 Wochen) auf den Beringungsstationen Bolle die Magadino, TI und Col du Bretolet, VS
1994/1995	Inventar der Nachtigallpopulation in der Petite Camargue Alsacienne (F), im Auftrag von Prof. H. Durrer, Universität Basel
	Anstellung als wissenschaftlicher Mitarbeiter (je 1 Monat) der Vogelwarte Sempach zum Sammeln von Singvogel-Blutproben auf den Beringungsstationen in der Coto de Donaña (ESP) und Gibraltar (UK)
1995	Beringerprüfung an der Vogelwarte Sempach
	Mitarbeit am Schweizerischen Brutvogelatlas (Bearbeiten von Quadraten im TI)
1998	Mitarbeit an populationsbiologischer Studie der Kohlmeise an der Vogelwarte Sempach
seit 2000	Projektleitung zweier ökologischer Vernetzungsprojekte im Oberbaselbiet (unterstützt durch die Walder-Bachmann-Stiftung & den Fonds Landschaft Schweiz)
2002-2005	Vorstandsmitglied von Pro Natura BL
seit 2006	Leitung eines Schwarzkopftragopan Monitoring und Conservation Projektes in Palas, North Western Province, Pakistan (im Auftrag der World Pheasant Association und des WWF Pakistan).
seit 2007	Mitglied des Stiftungsrates der World Pheasant Association
	Mitglied der Pheasant Specialist Group von IUCN
	Senior Researcher beim Game and Wildlife Conservation Trust, England

Further Activities

1996-2000	Präsident des Uniorchester Basel
2000-2002	Kassier des Uniorchester Basel
seit 2002	Aktiv-Mitglied des SAC Basel (Hoch-, Ski- & Schneeschuhtouren)

.

PUBLICATIONS

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Verwendung ganz alter Rebhühner

Der alten Hähne Wildbret

Ist hart und zähe, aber fett.

Von jungen ist es zart und weich,

'ne Speise für das Himmelreich.

Ein junges Huhn erkennt man d'ran,

dass gelb sich sieht sein Ständer an.

Sein Schnabel ist von hellem Braun

Und ziemlich weisslich anzuschaun.

Ist dieser hell, der Ständer grau,

Dann rate Deiner lieben Frau,

Sie brat es nicht zum eignen Schmaus,

Sie send' es in des Nachbars Haus.

Doch hast gepachtet Du 'ne Jagd,

So sei Dir dringend hier gesagt,

Die alten Hähn dem Dorfschulz sende

Und spar durchaus nicht mit der Spende.

Denn kommt die Neuverpachtung dann,

So sagt er Dir im Voraus an:

Die Pacht ich Ihnen prolongier',

Sie bleiben Pächter vom Revier.

Noch besser aber kannst Du thun,

Du schenkst jedwedes alte Huhn

Der bitterbösen Schwiegermutter,

Das ist für Sie das beste Futter.

Aus: Von Schiedeberg, R. (1896). Das Rebhuhn, seine Naturgeschichte, künstliche Aufzucht, Jagd und Fang. Paul Parey, Berlin.

Photos:
Page 85:   Markus Jenny
Page 89:   top – Arthur Scott, others – Markus Jenny
All others: Francis Buner

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The Swiss Ornithological Institute
is a non-governmental scientific research institute at Sempach, near Lucerne. It was founded in 1924, mainly as a centre to organise and coordinate bird ringing in Switzerland and to study bird migration. Since 1954 the SOI has been a private foundation for ornithology, supported by donations and subscriptions from the Swiss population. It nowadays covers a wide range of topics from bird migration and ecology to population monitoring and applied studies for landscape management and conservation. The SOI employs about 80 members of staff on 60 full-time jobs. It works together with about 1000 volunteer ornithologists and ringers throughout Switzerland. The institute in Sempach accommodates an ornithological library with more than 250 journals and 7000 books.

The projects of the Swiss Ornithological Institute are grouped in four programmes ranging from basic research to applied projects:

The programme **Population Monitoring** aims at monitoring changes in the size and distribution of bird populations in Switzerland in order to provide the basis for conservation and for detailed causal analysis. The monitoring programmes rely to a great extent on the collaboration of about 1000 volunteers. Databases hold long-term data for the whole of Switzerland.

Ecological studies focus on endangered species and habitats. How do species breeding in forests and in farmland use specific habitats and their food supply, where are the bottlenecks in their breeding ecology and how do they affect their breeding success? The results are a basis for landscape management.

Research on **Bird Migration** uses methods such as ringing, censusing, infrared and radar observations, as well as physiological studies, to study the influence of environmental conditions on bird migration, with particular emphasis on barrier crossing.

Applied Projects use the results of scientific studies to suggest measures in landscape planning and management and to test their effects. A special focus lies on measures to improve habitats in agricultural areas.

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