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Beiträge zur Biologie und zum Schutz des Rebhuhns (*Perdix perdix* Linné 1758)

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Kapitel I

Einleitung

Einleitung

Das Rebhuhn oder Feldhuhn (*Perdix perdix* Linné 1758) gehört innerhalb der Ordnung der Hühnervögel (*Galliformes*) der Familie der Hühner (*Phasianidae*) und der Unterfamilie der Glattfoothühner (*Phasianinae*) an. In seinem weiten paläarktischen Verbreitungsgebiet kommt es in neun Unterarten vor.

Das Rebhuhn ist ein kleiner gedrungener ca. 300 bis 400 g schwerer Hühnervogel, in dessen lebhaft gefärbten Gefieder braune und graue Farbtöne abwechslungsreich gemustert vorherrschen. Das von weitem unscheinbare Gefieder ist eine Anpassung an das kryptische Leben als Bodenvogel, der im Durchschnitt weniger als eine Minute pro Tag fliegt.



Abb. 1: Rebhuhnkette Deckung suchend in einer Feldhecke (Foto: M. Jenny)

Die Paarungszeit der Rebhühner liegt im Frühjahr zwischen Anfang März und Ende April. Die etablierten Paare verteidigen ihr Revier vor allem bei Sichtkontakt gegen ihre Artgenossen. Ab Ende Februar markiert insbesondere der Rebhahn sein Revier durch weithin hörbare Rufe während der Abend- und Morgendämmerung. Als Bodenbrüter legen die Rebhennen ihr aus im Durchschnitt 15 Eiern (Literatur dazu in Dwenger 1991, Glutz von Blotzheim & Bauer 1994) bestehendes Gelege in Gras-,

Kraut- oder Feldfruchtbeständen an. Bei Verlust des Erstgeleges, kann noch ein Ersatzgelege produziert werden, das im Durchschnitt noch aus 11 Eiern besteht. Nach ca. 24-tägiger Bebrütung allein durch die Henne schlüpfen weitgehend gleichzeitig die Dunenküken, die anschließend gemeinsam von dem monogamen Paar geführt werden. Der Familienverband, die sogenannte Kette, ist bis zur Balzzeit des folgenden Frühjahrs eine stabile soziale Einheit, deren Raum- und Zeitverhalten völlig synchronisiert ist. Kleine Ketten oder Brutpaare ohne Reproduktionserfolg schließen sich anderen Ketten an oder schließen sich zu solchen Kleingruppen mit ca. 5-20 Individuen im Herbst zusammen (Blank & Ash 1956). Als Stand- oder Strichvogel überwintern Rebhühner überwiegend im sommerlichen Aktionsraum. Die Ausdehnung der „home range“ ist ausgesprochen variabel beispielsweise in Abhängigkeit von der Verfügbarkeit benötigter Ressourcen, vom Störungs- und Prädationsregime oder auch von der Populationsdichte. Im Winter umfasst das Streifgebiet im Durchschnitt 11.08 (Döring & Helfrich 1986) bzw. 14 ha (Buner et al. 2005). Die relative Standorttreue ist nicht zuletzt bedingt durch den mindestens neunmonatigen Zusammenhalt der Familie, der die Tradierung von ortsspezifischen Verhaltensweisen fördert (Wübbenhorst 2002).

Als Art, die ihre evolutive Ausprägung in Steppen erfahren hat, findet das Rebhuhn sekundären Lebensraum in offenen Ackerbau-betonten Agrarlandschaften Mitteleuropas, die es im Regelfall bis in Höhen von 500-600 m ü. M. und gebietsweise auch darüber hinaus bewohnt (Glutz von Blotzheim & Bauer 1994). Das Rebhuhn bevorzugt kleinflächig strukturierte Ackerlandschaften mit entsprechend hohem Anteil an permanenten Randstrukturen, wie Altgrasstreifen, Grabenböschungen oder Hecken, Brachen und großer Feldfruchtvielfalt.

Wie alle anderen typischen Feldvögel der Agrarlandschaft (Donald 2006, Butler 2007, Reif et al. 2008) hat auch das Rebhuhn insbesondere in den letzten 30 Jahren einen massiven Bestandseinbruch um oft mehr als 90 % in weiten Bereichen seines Verbreitungsgebietes erlitten (vgl. Gossow et al. 1992, Tucker & Heath 1994, Potts 1997). Die Dramatik des Rückgangs hat insbesondere in den letzten drei Jahrzehnten dazu geführt, dass schwerpunktmäßig Untersuchungen zur Aufklärung der Rückgangsursachen durchgeführt wurden und resultierende Erkenntnisse in entsprechende naturschutzfachliche Konzepte zur Wiederansiedlung oder zur Lebensraumaufwertung eingeflossen sind (e.g. Buner et al. 2005, Tillmann & Kinser 2007, Buner & Schaub 2008). Insbesondere die Veränderung der Agrarlandschaft durch die Modernisierung der Landwirtschaft nach dem zweiten Weltkrieg wird in ihren direkten

und indirekten Wirkungen auf die demographischen Variablen des Rebhuhns für seinen Rückgang verantwortlich gemacht (Tucker & Heath 1994, Bauer & Berthold 1996). Jedoch sind die kausalen Zusammenhänge zwischen Bestandseinbruch und Veränderung des Lebensraumes komplex und wurden von unterschiedlichen Autoren unterschiedlich bewertet (Wübbenhorst & Leuschner 2006). Der vielfach beschriebene Schlüsselfaktor der Qualität eines Rebhuhnlebensraumes scheint die strukturelle Diversität einer Landschaft zu sein, die sich in erster Linie in der Dichte von Grenzlinien und ruderalen Flächen darstellt (e.g. Rands 1986, Glänzer et al. 1993, Mooij 1997, Panek & Kamieniarz 2000). Als negativen Einfluss auf die Ernährungssituation und damit die Vitalität der Küken führen z.B. Southwood & Cross (1969), Potts & Aebischer (1997) oder Moreby & Southway (1999) den effizienten Einsatz von Pestiziden an. Der Mangel an geeigneten Nistplätzen wird vor allem von Potts (1980) und Wübbenhorst & Leuschner (2006) als die Abundanz limitierender Faktor identifiziert. Darüber hinaus wird der Prädation eine Bedeutung in der Populationsdynamik des Rebhuhns zugeschrieben (e.g. Potts 1986, Tapper et al. 1996, Watson et al. 2007 a, b).

Das Ziel der vorliegenden Arbeit ist es, das Wissen um die Ökologie des Rebhuhns in der Agrarlandschaft um bisher nicht beschriebene Aspekte zu ergänzen und Empfehlungen zur Lebensraumverbesserung und zu einem flächendeckenden Populationsmonitoring zu geben.

Einführend werden in einem naturschutzfachlichen Ansatz in **Kapitel II** vor dem Hintergrund des ökologischen Profils des Rebhuhns seine Ansprüche an die Physiognomie und Gestaltung von Ansaatbrachen beschrieben. Allgemeine Grundzüge der Ökologie und kritische Faktoren in der Populationsdynamik des Rebhuhns werden dargestellt, und darauf aufbauend wird seine Situation in den heutigen Agrarlandschaften diskutiert. In die Arbeit sind neben der umfangreichen Literatursichtung im Rahmen des von der Deutschen Bundesstiftung Umwelt (DBU) geförderten Projektes „Lebensraum Brache“ Erkenntnisse aus dem Monitoring der Rebhuhnpopulationen in den entsprechenden Untersuchungsgebieten in Bayern und Hessen eingeflossen. Innerhalb dieser Untersuchungsgebiete wurden Ackerbaugebiete mit einem Brachflächenanteil von ca. 5 % solchen vergleichend gegenübergestellt, in denen keine Brachen vorhanden waren.

Insbesondere Ackerbrachen und physiognomisch vergleichbare Ruderalvegetation können eine herausragende Bedeutung als vielseitige Bereicherung in den Vor-

kommensgebieten des Rebhuhns einnehmen, wie in verschiedenen Studien zur Habitatwahl des Rebhuhns gezeigt werden konnte (e.g. Kaiser & Storch 1996, Salek et al. 2004, Buner et al. 2005, Tillmann & Kinser 2007, Salek & Marhoul 2008, Henderson et al. 2009). Bei Vorhandensein von Ackerbrachen werden diese bevorzugt als Nisthabitat, Nahrungshabitat und Deckungshabitat genutzt und haben damit einen prägenden Einfluss auf das Raumzeitverhalten des Rebhuhns. Brachen stellen im Regelfall eine mehrjährige damit quasi permanente, nicht lineare Struktur dar, die entsprechende Qualitäten bietet. So ist im Frühjahr zur Balzzeit des Rebhuhns das Vorhandensein von „sicheren“ Nistplätzen ein bedeutender Faktor, der die Brutpaardichte eines Lebensraumes mitbestimmt (Rands 1987, Wübbenhorst & Leuschner 2006). Wie Tillmann & Kinser (2007) zeigen, werden Brachen bevorzugt als Nistplatz genutzt. Im Vergleich zu linearen Randstrukturen, denen die Wirkung einer ökologischen Falle zugeschrieben wird (Tryanowsky 2000, Evans 2004), können vergleichsweise großflächige Brachen das Prädationsrisiko streuen und bieten damit einen relativ sicheren Nistplatz. Zusätzlich bieten Brachen aufgrund der Pflanzenvielfalt, dem Bestand des Aufwuchses über den Winter und aufgrund der ausbleibenden Bodenbearbeitung einer reichhaltigen Arthropodenfauna einen Lebensraum. Arthropoden wiederum sind essentiell für die Ernährung der Küken insbesondere während der ersten drei Wochen nach dem Schlupf. Die Überlebensrate der Küken ist einer der Schlüsselfaktoren im Populationsgeschehen des Rebhuhns (Potts 1986, Aebischer & Julie 2004, Moreby et al. 2006). Darüber hinaus konnte in verschiedenen Studien gezeigt werden, dass Brachen und höhere Vegetation insbesondere am Tag, wenn die hauptsächliche Prädationsgefahr von Greifvögeln ausgeht, bevorzugt als Deckung aufgesucht werden, da sie dem Rebhuhn Sicherheit vor Attacken aus der Luft bieten (Glänzer et al. 1996, Salek et al. 2004, Watson et al. 2007)

Im Abgleich mit dem ökologischen Profil des Rebhuhns werden die Ansprüche an den Charakter von Aufwüchsen auf Brachen im Detail diskutiert und Empfehlungen zur Integration und Anlage von Ansaatbrachen im Rahmen von Schutzkonzepten gegeben. Ansaatbrachen sind aktiv begrünzte Äcker. Die verwendeten Saatgutmischungen setzen sich aus Kulturpflanzen und / oder autochthonen Wildpflanzen zusammen, wobei die Artenzusammensetzung an der anvisierten Standzeit der Brache ausgerichtet wird. Die so begrünzten Brachen stellen eine landwirtschaftlich akzeptable Form der Flächenstilllegung dar, da sie ein dominantes Aufkommen von „Problemunkräutern“ unterdrücken können und im Anschluss an die Brachephase ohne erhöhten Unkrautdruck wieder in die landwirtschaftliche Nutzung überführt

werden können – dies steht häufig im Gegensatz zu Sukzessionsbrachen auf wüch-sigen Standorten. Optimal sollten Ansaatbrachen schütterere Vegetation aufweisen, die dem Rebhuhn als Bodenvogel Bewegungsfreiheit beispielsweise im Rahmen der Nahrungssuche oder der Feindvermeidung erhält. Zur weiteren Erhöhung der struk-turellen Diversität auf den Brachen wird vorgeschlagen, diese durch gegrubberte Streifen aufzulockern und so die Randliniendichte zu erhöhen. Wie Jenny et al. (2002) zeigen, sollte dann der Abstand zwischen solchen Flächen nicht mehr als 800 m und ihr Anteil an der Offenlandfläche mindestens 5 % betragen, um einen positi-ven Effekt auf die Rebhuhnpopulation zu erzielen. In diesem einleitenden Kapitel wird damit das Rebhuhn in seiner Eignung als „Regenschirmart“ für die Feldvogel-gemeinschaft, darin insbesondere für die bodenbrütende Gilde, herausgestellt. In Artenschutzplanungen in der Agrarlandschaft lässt sich ein breites Spektrum typi-scher Arten fördern, indem lebensraumverbessernde Maßnahmen, wie die Anlage von Ansaatbrachen, durchgeführt werden.

In **Kapitel III** wird in einem empirischen Ansatz das Verhalten des Rebhuhns bzw. der Rebhuhn-kette bei Nacht im Winter dargestellt und analysiert. Während die Öko-logie des Rebhuhns am Tage umfassend beschrieben ist, war es Ziel dieser Arbeit die „Nachtökologie“ des Rebhuhns systematisch zu erfassen und vergleichend mit der Situation am Tage zu interpretieren. Im Rahmen einer umfangreichen Literatur-recherche und der Befragung von Experten auf dem Gebiet der Rebhuhnökologie konnten keine Informationen zu dessen Verhalten in der Nacht gefunden werden. Damit verblieb bisher quasi die Hälfte des Lebens des Rebhuhns bis zu dieser Stu-die unbeschrieben. Die Arbeit soll insbesondere vor dem Hintergrund des extremen Bestandsrückgangs in den letzten 30 Jahren (Bro et al. 2001, Aebischer & Ewald 2004, De Leo et al. 2004, Panek 2005) dazu beitragen, das Wissen um die Reb-huhnökologie zu komplettieren und mögliche Besonderheiten des nächtlichen Feind-vermeidungs-, Sozial- und Habitatnutzungsverhalten aufzudecken. Die Schlafplatz-wahl sollte in Hinblick auf den Charakter der Vegetation dargestellt und so unter an-derem die Bedeutung von Brachflächen in der Nacht untersucht werden.

Dabei wird insbesondere der Hypothese nachgegangen, dass sich die Präferen-zen in der Habitatnutzung und die Strategien zur Feindvermeidung zwischen Tag und Nacht unterscheiden und die Schlafplatzwahl primär ein Resultat optimierter Feindvermeidung ist. Nicht-letale Effekte eines immanenten Prädationsrisikos prä-

gen in der Regel das Raum-Zeit-Verhalten von Beutetieren bedeutend (vgl. Tryjanowski et al. 2002, Creswell 2008).

Mittels moderner Thermographie konnten erstmalig das Ruheverhalten, das Sozialverhalten, die Habitatpräferenzen sowie das Feindvermeidungsverhalten beschrieben werden. Es wurden dazu Untersuchungsgebiete ausgewählt, die sich durch eine vergleichsweise hohe Rebhuhndichte auszeichneten, um den Suchaufwand in der Nacht zu minimieren. Insgesamt konnten 640 Rebhühner detektiert und ihr Verhalten aufgenommen und anschließend anhand der Videoaufnahmen analysiert werden. Im Gegensatz zur Raumnutzung am Tag (vgl. Döring & Helfrich 1986, Pegel 1987, Glänzer et al. 1993, Buner et al. 2005) meidet das Rebhuhn in der Nacht ganz klar Randstrukturen wie Hecken, Altgrasstreifen, Grabenböschungen und Vegetation, die höher als 12 cm ist, um im Mittel 60 m vom Rand entfernt im offenen Feld seinen Schlafplatz zu finden. Rebhühner attribuieren offensichtlich bestimmte Landschaftselemente, insbesondere lineare Randstrukturen, mit einem höheren Prädationsrisiko bzw. einer höheren Störungsfrequenz und versuchen, diesen Risiken räumlich auszuweichen. Die erhöhte Aktivität von Prädatoren und die gesteigerte Störfrequenz durch andere nachtaktive Säugetiere entlang von Randstrukturen wird von verschiedenen Autoren aufgezeigt (e.g. Tryjanowski 2000, Bro et al. 2004, Evans 2004). Das nächtliche Raumverhalten des Rebhuhns stellt sich hier als optimierte Anpassung an die von ihm empfundene Prädationsrisiko-Landschaft dar („predation risk landscape“ sensu Thomson et al. 2006). Darüber hinaus kann hier der Begriff Prädationsrisiko-Zeitplan („predation risk schedule“) geprägt werden: Wird das Raumverhalten am Tag mit dem in der Nacht verglichen, so ist eine zusätzliche zeitliche Komponente zu erkennen. Tagsüber geht die vornehmliche Gefahr für das Rebhuhn von Greifvögeln aus, vor denen es in höherer Vegetation und Randstrukturen Schutz sucht (vgl. Glänzer et al. 1993, Salek et al. 2004). Nachts dagegen sind terrestrische Prädatoren wie z.B. der Rotfuchs (*Vulpes vulpes*) die Hauptgefahr, die besonders in und an den am Tage zum Schutz aufgesuchten Randstrukturen aktiv sind, die nachts folgerichtig vom Rebhuhn gemieden werden. Zusätzlich konnte gezeigt werden, dass Rebhühner in dunkleren Nächten weiter von den Randstrukturen entfernt ihren Schlafplatz einnehmen. In solchen Nächten können sie sich nur noch eingeschränkt auf den Gesichtssinn bei der Feinderkennung verlassen (vgl. Beauchamp & McNeil 2003). Außerdem sind terrestrische Prädatoren in dunklen Nächten aktiver (vgl. Shapira et al. 2008), so dass die Sicherheit der Rebhühner mit zunehmender Distanz vom Rand steigt. Weiterhin wird in Kapitel III gezeigt, dass die Rebhühner einer

Kette in kalten Nächten zur Reduzierung der individuell exponierten Körperoberfläche eng zusammenrücken. Bevorzugt ruhen sie allerdings in Kleingruppen von 2 bis 3 Individuen, vermutlich um den Gesichtssinn effizienter einsetzen zu können. Die Bedeutung des Gesichtssinns bei der Feinderkennung wird durch die Verlängerung der Fluchtauslösedistanz (FID) bei helleren Sichtverhältnissen in der Nacht bestätigt. Ebenfalls verlängert sich die FID mit zunehmender Anzahl von Rebhühnern in der Schlafgemeinschaft. Diese Erkenntnis stimmt überein mit Untersuchungen an anderen Arten, die in Gruppen potentielle Fressfeinde früher erkennen, wobei jedem Individuum eine im Vergleich zu kleineren Gruppen vermehrte Zeit für Komfortverhalten zur Verfügung steht (sensu „many-eyes hypothesis“, Lima 1995). Die gemessene durchschnittliche Fluchtauslösedistanz von 22,8 m bestätigt eine erfolgreiche Feindvermeidung.

Der erstmalige Einsatz der Wärmebildtechnik zur Detektion und Kartierung ruhender Rebhühner und zur Analyse des nächtlichen Verhaltens des Rebhuhns in der offenen Agrarlandschaft hat sich als ausgesprochen effizient erwiesen. Selbst Detailspekte konnten dadurch erstmalig beschrieben und interpretiert werden. In diesem Kontext hat sich das Defäkationsverhalten fliehender Rebhühner als besonders erwähnenswert herausgestellt und wird in **Kapitel IV** gesondert behandelt. Ausgehend von dem empirischen Befund, dass Rebhühner während des Fluchtfluges im Regelfall defäkieren, wird die Hypothese aufgestellt, dass dieses Verhalten von der parasympathisch gesteuerten Angstdefäkation evolutiv abgekoppelt ist, da es verschiedene selektive Vorteile mit sich bringt. Diese werden vor dem Hintergrund ökologischer Anpassungen anderer Tierarten interpretiert, die ebenfalls die Defäkation aktiv in bestimmte Verhaltensweisen einbinden. Für einige Vogelarten wurde bereits beschrieben, wie Exkremente neben der Beseitigung metabolischen Abfalls aktiv in defensive bzw. protektive Verhaltensweisen eingebunden werden und damit eine zusätzliche Bedeutung erhalten. Als prominentes Beispiel in diesem Zusammenhang kann das aggressive Bekoten von Nestprädatoren insbesondere durch die Wacholderdrossel (*Turdus pilaris*) aber auch durch die Singdrossel (*Turdus philomelos*), die Misteldrossel (*Turdus viscivorus*) oder die Flusseeeschwalbe gelten (vgl. Mester 1976, Nisbet 1983, Hogstad 2004). Bei einigen Schnepfenvögeln (*Scolopacidae*) und Entenvögeln (*Anatidae*) bekotet der brütende Altvogel sein Gelege direkt vor der Flucht, wenn sich potentielle Nestprädatoren nähern. Simmons (1955) und Mester (1976) schreiben diesem Verhalten aufgrund des penetranten Geruchs eine ab-

schreckende und damit protektive Wirkung zu, wodurch in vielen Fällen das Gelege gerettet wird.

Die Ausweichbewegung der Rebhühner einer Kette findet nachts in der Regel synchron statt. In den meisten Fällen fliegen dabei alle Rebhühner direkt aus der Ruheposition auf. Dieses Verhalten ist gegensätzlich zu dem am Tag, wenn Rebhühner sich Störungen oder potentiellen Fressfeinden gerne auch auf dem Boden laufend entziehen und so Deckung aufsuchen. Nachts bei der vornehmlich terrestrischen Prädationsgefahr wählt das Rebhuhn fast ausschließlich den Fluchtflug, um Fressfeinden zu entgehen. Es konnte erstmalig beobachtet werden, dass Rebhühner auf den ersten Metern des Fluchtfluges in den meisten Fällen jeweils mehrmals defäkieren. Steigt eine Rebhuhnkette von mehr als 10 Individuen auf, so stellt sich dieses Verhalten auf den thermographischen Aufnahmen wie ein Regenschauer dar, der auf einer Fläche von ca. 200 m² niederschlägt. Die Ausprägung dieser Verhaltensweise erwies sich als unabhängig von allen anderen aufgenommenen Variablen. Bei der gemessenen durchschnittlichen Fluchtauslösedistanz von 22,8 m kann dieses Defäkationsverhalten nicht mehr mit der parasymphisch stimulierten Angstdefäkation in Zusammenhang stehen. Die Angstdefäkation tritt bei den meisten Vertretern in direkt lebensbedrohlicher Situation auf, etwa bei direktem Körperkontakt mit dem Fressfeind oder wie aus der Ornithologie bekannt, bei dem Handling zu geringerer Vögel (vgl. Ricklef 1977).

Wie bei anderen Arten bereits gezeigt, kann die Defäkation auch beim fliehenden Rebhuhn abschreckende Wirkung auf attackierende Fressfeinde haben und den synchronen Start der Rebhühner in seinem Konfusionseffekt zusätzlich unterstützen. Bei der ermittelten durchschnittlichen Fluchtdistanz des Rebhuhns von im Mittel 125,71 m wäre der sich olfaktorisch orientierende Fuchs als Hauptgefahr für das Rebhuhn (Reynolds & Tapper 1995) durchaus in der Lage, den neuen Schlafplatz der Rebhühner aufzufinden. Die frisch ausgeschiedenen Exkremente könnten eine olfaktorische Blendung bewirken und das Auffinden des neuen Standortes der Rebhühner erschweren. Darüber hinaus wird durch das Defäkieren während der initialen Phase des Fluchtfluges das Ausscheiden von Kot am neuen Ruheplatz verzögert und damit auch die Produktion von attrahierenden Geruchsquellen. Lilliendahl (2000) beschreibt für Grünfinken (*Carduelis chloris*) das gleiche Verhalten und vermutet, dass das Beschleunigungsvermögen erhöht wird und so das Entkommen erleichtert wird. Die Reduktion des Gewichtes führt zu einer Energieeinsparung, die unabhängig von der Prädationsgefahr einen selektiven Vorteil bedingen kann. Im Rahmen

dieser Studie konnte die Reduzierung des Fluggewichtes durch die Defäkation auf im Mittel 1,1 % des Körpergewichtes von Rebhühnern bestimmt werden. Es wird angenommen, dass damit der selektive Vorteil marginal ist, im Laufe der Evolution dieses Verhalten aber durchaus positiv selektiert wurde.

Die Erkenntnisse aus dieser Studie unterstützen die Hypothese, dass das beschriebene Defäkationsverhalten, ohne zusätzliche energetische Kosten zu verursachen, verschiedene selektive Vorteile mit sich bringt. Dieses Verhalten als ursprünglich parasymphatische Reaktion auf eine Gefahr scheint sekundär funktionell in den Komplex des Feindvermeidungsverhaltens durch Selektion eingebunden worden zu sein. Es werden weitere Untersuchungen zur Klärung der Selektionsmechanismen empfohlen.

Um optimierte Entscheidungen hinsichtlich des Schutzes und auch der Bejagung des Rebhuhns in Deutschland treffen zu können oder auch den Erfolg von Schutzmaßnahmen, wie sie z.B. im Rahmen von Agrarumweltprogrammen realisiert werden, bewerten zu können, ist ein flächendeckendes Monitoring unabdinglich. Auf dieser Basis können der Populationsstatus und die Populationsdynamik des Rebhuhns aufgezeigt werden und vor diesem Hintergrund die relevanten Einflussgrößen identifiziert und interpretiert werden.

Im abschließenden **Kapitel V** wird die Leitfrage verfolgt, ob Schätzungen von Jägern zu der Anzahl der in ihrem Jagdrevier vorhandenen Rebhuhnpaare ein zuverlässiger Indikator für die Analyse des Populationsstatus und der Populationsdynamik auf großer Fläche ist. Vor Verwendung von Schätzdaten im Bereich der Ökologie, die mit Hilfe von Fragebögen generiert werden, ist grundsätzlich eine kritische Evaluierung vor Verwendung erforderlich (White et al. 2005). Zur Evaluierung der in Niedersachsen im Rahmen der Wildtiererfassung Niedersachsen (WTE) gewonnenen nahezu flächendeckenden Bestandsschätzungen der Jäger wurden im Rahmen dieser Studie in 123 zufällig ausgewählten Revieren flächendeckend standardisiert die Rebhuhnbrutpaare erfasst und in Relation zu den Schätzungen der Jäger diskutiert.

Insgesamt wurden während der Projektlaufzeit von fünf Jahren auf einer Fläche von 63.847 ha detailliert die Rebhuhnvorkommen kartiert. An diesen Kartierungen nahmen an den 255 Kartierterminen 1.978 Personen teil. Im Vergleich dieser detaillierten und standardisierten Kartierungen mit den entsprechenden Schätzungen der örtlichen Jäger konnte gezeigt werden, dass die Jäger tendenziell die Rebhuhndich-

te in den von ihnen betreuten Jagdrevieren leicht unterschätzen. Die Unterschätzung von Dichten von Wildtierpopulationen durch Amateure entspricht einem bekannten Phänomen (vgl. Genet & Sargent 2003, Newmann et al. 2003). Bei niedrigen Rebhuhndichten war die Übereinstimmung von der Kartierung und der Schätzung der Jäger vermutlich aufgrund der übersichtlicheren Verhältnisse besser; bei höheren Dichten war dagegen die Diskrepanz größer. Die Abweichung nahm ebenfalls zu, je größer das Jagdrevier war. Dies kann auf die relativ verringerte Flächenpräsenz des betreuenden Jäger zurückgeführt werden. Im Vergleich zu anderen Studien kann die Abweichung der Schätzungen der Jäger von den detaillierten Kartierungen als akzeptabel bewertet werden. Als ein wichtiger Grund für die relativ gute Kenntnis der Jäger über den Rebhuhnbrutbestand in ihrem Jagdrevier ist in deren professionellen und sozialen Umfeld zu finden. So waren ein Großteil der Jäger die örtlichen Landwirte oder zumindest gesellschaftlich in den landwirtschaftlichen Kontext eingebunden. Durch die örtliche Verbundenheit und die landwirtschaftliche Aktivität hat diese Bevölkerungsgruppe eine gute Kenntnis ihrer Umwelt (vgl. Reading et al. 1996). Obwohl die Beobachtungen der Jäger zufällig sind und sie die Rebhühner nicht konsistent nach einer standardisierten Methode erfasst haben, ergeben die einzelnen Beobachtungen im Laufe des Jahres einen guten Überblick über die lokale Rebhuhnpopulation. Es wird angenommen, dass eine passive Standardisierung der Erfassung aufgrund der ähnlichen Interessen, ähnlichen Berufe und ähnlichen Präsenzphasen der befragten Jäger gewährleistet ist. Die WTE als alljährliche Briefumfrage kann nach dieser Erkenntnis Grundlagendaten zur Populationsdynamik des Rebhuhns in Niedersachsen liefern und Populationsentwicklungen in Abhängigkeit von Umweltveränderungen aufzeigen. Die Verwendung beispielsweise zur Evaluierung von Agrar-Umweltmaßnahmen bietet sich damit an. Darüber hinaus hat die Befragung der Jäger den Effekt, diese für die Schutzbedürftigkeit des jagdlich kaum mehr relevanten Rebhuhns zu sensibilisieren.

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Kapitel II

**Das ökologische Profil des Rebhuhns
(*Perdix perdix* L.)
und Konsequenzen für die Gestaltung von
Ansaatbrachen zur Lebensraumverbesserung.**

Tillmann J.E. (2006)

Beiträge zur Jagd- und Wildforschung 31, 265-274

Einführung

Die Bewertung der Qualität, der Kondition und des Status von Vegetation in ihrer Eigenschaft als lebensraum-gestaltendes Element ist ein wichtiger Bestandteil in ökologischen Studien. So wird die Vegetation im Hinblick auf die Eignung als Lebensraum bzw. Nahrung für bestimmte Tierarten bewertet. Umgekehrt kann das ökologische Anspruchsprofil von Tierarten quasi als Stempel in Artenschutzplanungen genutzt werden, um idealtypische Lebensraumrequisiten in die Fläche zu projizieren und daran lebensraumverbessernde Maßnahmen auszurichten. Auf die Vegetation bezogen bedeutet dies, dass in artbezogenen Konzepten zur Lebensraumgestaltung Empfehlungen zur Physiognomie, zur Artenvergesellschaftung und zur Bestandesdichte gemacht werden. In Agrarökosystemen, beispielsweise bei der Anlage bestimmter Brachetypen, sind neben den genannten Punkten noch Empfehlungen zum Bewirtschaftungsregime darzustellen, das den gewünschten Status auch in Abhängigkeit von Naturraum und Jahreszeit herstellen und evtl. über einen längeren Zeitraum erhalten kann.

Ausgehend vom ökologischen Profil des Rebhuhns (*Perdix perdix* L. 1758) sollen hier Empfehlungen zur Gestaltung von Ansaatbrachen als agrarwirtschaftlich akzeptable Form der Flächenstilllegung diskutiert werden. Das Rebhuhn gilt als Charakterart in Agrarlandschaften. Es hat in den letzten 50 Jahren aufgrund veränderter Landnutzungsmodalitäten massive Bestandseinbrüche in seinem gesamte Mitteleuropäischen Verbreitungsgebiet erlitten (e.g. De Leo et al. 2004 und Quellen darin) Mit seinen ökologischen Ansprüchen kann es als Repräsentant für typische Arten der Ackerlandschaften gelten. Von Schutzbemühungen um das Rebhuhn als Schirmart (*sensu* Lambeck 1997) können eine Vielzahl anderer Arten profitieren. Überdies lässt sich die Öffentlichkeit über das charismatische Flaggschiffart Rebhuhn für die Natur der Agrarlandschaft sensibilisieren.

Das Rebhuhn gilt als Kulturfolger und Bewohner offener Landschaften (e.g. Potts 1986, Dwenger 1991). Sein ursprüngliches Vorkommen beschränkte sich auf offene Landschaften mit Pflanzenvergesellschaftungen niedriger Höhe – in erster Linie Steppen, Heiden, offene Buschlandschaften (Glutz von Blotzheim & Bauer 1994). Mit sich ausbreitender In-Kulturnahme der Landschaften durch Ackerbau und Weidewirtschaft in Europa seit dem Neolithikum fand das Rebhuhn in diesen Kulturlandschaften Ersatzlebensraum oder vielmehr zusätzlichen Lebensraum. Dies gilt insbesondere für die Nominatform. Die Unterart *P. p. sphagnetorum* A. war unter Umstän-

den in Deutschland schon vor den großflächigen Landschaftsveränderungen durch den Menschen heimisch und bewohnte natürliche Offenhabitate wie die Randbereiche von Hochmooren (Bräsecke 2002). Diese Unterart kann heute als ausgestorben gelten; evtl. bestehen im Emsland und Münsterland Mischpopulationen der beiden Unterarten. Peters et al. (1972) und Teichert & Lepiksaar (1977) weisen aufgrund ihrer Funde darauf hin, dass das Rebhuhn mindestens seit der Bronzezeit in Europa heimisch ist.

Ehemalig waldbetonte Landschaften, die sich durch die Aktivitäten des Menschen hin zu Offenlandschaften entwickelten, wurden für die Art besiedelbar. In extensiv genutzten Kulturlandschaften wurden und werden auch heute noch Populationsdichten erreicht, die mitunter über denen liegen, die sie in natürlichen Ökosystemen erreichen (Dwenger 1991).

Mit der Intensivierung der Landwirtschaft in Deutschland und einhergehend mit den landschaftsstrukturellen Veränderungen sind die Populationsdichten des Rebhuhns jedoch in vielen Regionen stark gesunken, teilweise sogar lokal ausgestorben. Das Rebhuhn, ehemals Profiteur der landwirtschaftlichen Erschließung von Waldlandschaften und nicht zuletzt großflächiger Entwässerungen, hat sich insbesondere in den letzten 50 Jahren vom Kulturfolger hin zum Kulturflüchter entwickelt. Bis in die 1950er Jahre werden für hervorragende Rebhuhnlebensräume in Deutschland noch Dichten von 20 bis 30 Brutpaaren pro 100 ha angegeben (s.a. Tillmann 2005); heute können Agrarlandschaften mit 5 bis 6 Brutpaaren pro 100 ha Offenland als hervorragend gelten (Eylert 2003), wobei solche Rebhuhndichten nur noch kleinstäumig und ausgesprochen selten vorkommen. Die durchschnittliche Dichte ist weit geringer.

Die Art und Intensität der heutigen Landeskultur bietet zumindest großflächig nicht mehr bzw. nur in verringerter Qualität und Quantität die vom Rebhuhn im Laufe seines Lebens benötigten Lebensgrundlagen. Die Lebensraumkapazitäten der heutigen Agrarlandschaft sind, gemessen am ökologischen Anspruch des Rebhuhns, reduziert. Die Ausstattung heutiger Agrarlandschaften entfernt sich zusehends von der „vergänger“ Ackerlandschaften und seinen ursprünglichen ahemeroben oder oligohemeroben Lebensräumen.

In der Vergangenheit beeinflussten brachliegende Flächen die Rebhuhnpopulationen in Mitteleuropa positiv. Brachephassen waren in historischen Landnutzungssystemen wie der vom Mittelalter bis in die zweite Hälfte des 19. Jahrhunderts praktizierten Dreifelderwirtschaft fester Bestandteil in Fruchtfolgen und dienten der Rege-

nerierung des Ertragspotentials des Bodens. Die Heterogenität der Brachen in sich und die Vielfalt ihrer Typen waren mit ein Grund für die hohe Biodiversität der Agrarlandschaft in dieser Zeit (Mühlenberg & Slowik 1997). Ihr heutiger „Einsatz“ für den Artenschutz bietet folglich verschiedene Ansatzpunkte (Tillmann 2004).

Im Rahmen der konjunkturellen Flächenstilllegung und von Agrarumweltprogrammen eröffnen sich Chancen für Schutzmaßnahmen für das Rebhuhn (vgl. Börner 2004). Eine Option, den Lebensraum Agrarlandschaft wieder zu bereichern und für das Rebhuhn attraktiver zu gestalten, ist die gezielte Begrünung von Brachen durch verschiedene Saatenmischungen aus Kulturpflanzen oder autochthonen Wildpflanzen. Über die Verbesserung des Lebensraumes lassen sich verschiedene demographische Variablen positiv beeinflussen und damit Populationen stabilisieren (Bro et al. 2000). Die Anlage von Ansaatbrachen kann sich steigend sowohl auf die winterliche Überlebensrate als auch auf die während der Brut auswirken, genauso wie sie den Reproduktionserfolg durch eine Verringerung der Zerstörungsrate von Gelegen und der Mortalität der Küken erhöhen kann.

Situation des Rebhuhns in der heutigen Agrarlandschaft

Die Ausprägung des grundsätzlichen Schemas der Ressourcennutzung hat das Rebhuhn in seiner Evolution erfahren. Die ökologische Plastizität ist beim Rebhuhn also weitestgehend durch die Entwicklung in Offenlandschaften vorgegeben. Im Rahmen der ökologischen Toleranz können sich Anpassungen an raumspezifische oder sich im Laufe der Zeit verändernde Standortfaktoren entwickeln. Bei starker Veränderung des Charakters der Agrarlandschaft allerdings, wie sie in den letzten 50 Jahren zu verzeichnen war, werden die Ansprüche des Rebhuhns kaum mehr gedeckt und seine Anpassungsfähigkeit überfordert. Nicht zu Unrecht diskutiert Bezzel (1991) vor dem Hintergrund der mitteleuropäischen Zivilisationslandschaft die Frage „Hühnervögel – ein auslaufendes biologisches Programm?“. Im folgenden werden einige in ihrer Bedeutung herausragende Aspekte der Ökologie des Rebhuhns vor dem Hintergrund der heutigen Agrarlandschaft dargestellt.

Nistplatz

Für das Fortbestehen einer Population ist das Vorhandensein von Reproduktionsstandorten und Nistplätzen von großer Bedeutung. Rands (1987) konstatiert, dass für Rebhühner die Attraktivität eines Raumes maßgeblich von der Dichte und Qualität von Nisthabitaten, in erster Linie lineare, nicht beackerte Strukturen wie Hecken,

Graswege und Feldraine bestimmt wird. Daraus resultiert, dass die räumliche Verteilung und die Dichte der Rebhuhnpopulation vornehmlich von der Dichte bevorzugter Nisthabitate abhängig ist (Panek 1997).

Nach McCabe & Hawkins (1946) und Szederjei et al. (1959) ist das Vorhandensein von trockenem Nistmaterial, besonders abgestorbener Grasvegetation, für die Wahl des Nistplatzes von Bedeutung. Ein Großteil der Nester ist in den Randzonen der Feldkulturen zu finden. Szederjei et al. (1959) finden in ihrer Untersuchung 47% der Nester in den Randzonen von 1-5 m der Feldkulturen; McCabe und Hawkins (1946) fanden in den Randzonen von 0-3 m 41 % der Nester. Die Wahl von Getreidefeldern als Nistplatz wird im allgemeinen als Ausweichbrutplatz beschrieben, der bei Mangel an den absolut bevorzugten altgrasreichen Standorten mit Ruderalcharakter gewählt wird (Kaiser & Storch 1996).

Die höchste Brutpaardichte wird in Bereichen erreicht, in denen die bevorzugten Nisthabitate – Brachflächen, breite Ackerrandstrukturen - in hoher Dichte vorhanden sind. Umliegende Bereiche mit geringerer Dichte an Nisthabitaten werden nur im Sinne eines „Senkenhabitats“ bei Populationsdruck aus den attraktiven Bereichen besiedelt, wobei solche Brutpaare in den suboptimalen Bereichen auch einen geringeren Reproduktionserfolg haben (Panek 1997, Sálek et al. 2004). Daraus lässt sich folgern, dass über eine Anreicherung der Landschaft mit Nisthabitaten zum einen ihre Lebensraumkapazität erhöht wird und zum anderen der Reproduktionserfolg gesteigert werden kann.

Nahrung

Die Diät der Rebhühner ist sehr vielseitig. Ihre Nahrungswahl variiert mit den standörtlichen Unterschieden im Angebot, in Abhängigkeit vom Alter, von der Jahreszeit und Witterung. Sowohl pflanzliche als auch tierische Nahrung wird aufgenommen.

Die Überlebensrate der Küken wird von vielen Autoren als Schlüsselfaktor im Populationsgeschehen des Rebhuhns angesehen (z.B. Potts 1986, Aebischer & Julie 2004). Das Überleben der Küken in den ersten drei Lebenswochen ist wiederum maßgeblich von der Versorgung mit Insektennahrung abhängig (Southwood & Cross 1969, Green 1984).

Ameisen (*Formicidae*), deren Larven und Puppen spielen in der Ernährung von Rebhuhnküken eine herausragende Rolle und sind damit ein bestimmender Faktor für den Reproduktionserfolg. Diese Artengruppe als bevorzugter Bestandteil der Diät von Rebhuhnküken hat im letzten Jahrhundert starke Bestandseinbrüche erlitten.

Sturm & Distler (2003) nennen als erstrangige Rückgangsursachen für Ameisen alle das Mikroklima der Neststandorte verändernden Faktoren; die meisten Ameisenarten Deutschlands bauen im Boden oder auf der Bodenoberfläche Dauernester und sind damit ortstreu. Regelmäßige Bodenbearbeitung verhindert die ganzflächige Besiedlung von Ackerflächen, genauso wie ein zu dichter, hoch aufgewachsener Pflanzenbestand etwa auf alten Brachen, der sich insbesondere auf thermophile Arten negativ auswirkt. In ihrer Untersuchung zur Ameisenfauna unterschiedlicher Habitats im Lahn-Dill-Bergland in Hessen finden Dauber & Wolters (2004) die höchste Ameisendiversität wie auch die höchste Abundanz an Ameisennestern in Ackerbrachen im Vergleich zu Wiesen und konventionell genutzten Äckern. In erster Linie ist das bedingt durch die ausbleibende Bodenbearbeitung sowie die lückigen und artenreichen Vegetationsbestände.

Durch die Ausdehnung und die Intensivierung des Herbizid- und des Insektizideinsatzes in der Landwirtschaft hat sich das Spektrum der Invertebraten verringert, und es haben sich die Dominanzverhältnisse in Arthropodengesellschaften verschoben. Seit den 50iger Jahren des letzten Jahrhunderts hat der Anteil von *Aphiden* in den Arthropodengemeinschaften von Getreideäckern zugenommen (vgl. Green 1984, Borg & Toft 2000). Borg & Toft (2000) zeigen in einem Fütterungsversuch, dass Rebhuhnküken signifikant an Vitalität einbüßen, werden sie einseitig mit der Haferblattlaus (*Rhopalosiphum padi*) gefüttert. Die optimale Ernährung der Küken kann nur durch die Vielfalt und die Auswahlmöglichkeit verschiedener Insekten garantiert werden, was die große Bedeutung der Diversität an Ackerwildkräutern und der damit assoziierten Arthropodengemeinschaft unterstreicht (vgl. Southwood & Cross 1969, Potts 1970, 1986, Serre & Birkan 1985, Rands 1985, Panek 1992). Nach Kotuntersuchungen von Küken im Freiland durch Green (1984) machen *Aphidae*, *Heteroptera* und *Coleoptera* bei in Getreidefeldern Nahrung suchenden Rebhuhnküken den größten Anteil an der Nahrung aus.

Ackerwildkräuter spielen neben den Getreidearten eine große Rolle in der Ernährung von Rebhühnern. Im Winter werden bevorzugt Raps- und Wintergetreideschläge zur Nahrungssuche genutzt. An pflanzlicher Nahrung werden sowohl Blätter, Wurzeln, Früchte und Samen gefressen. Die Küken fressen in Ergänzung der Arthropodennahrung nach Green (1984) je nach Standort, Feldfrucht und typischerweise assoziierter Ackerwildpflanzengesellschaft die Samen verschiedener Gräser wie *Poa annua*, *Agrostis gigantea* und die von Kräutern wie *Stellaria media*, *Polygonum spp.* und *Fumaria officinalis*. Wildkrautsamen und Grassamen spielen auch in

der Ernährung der Altvögel besonders im Winterhalbjahr eine herausragende Rolle.

R-selektive Lebensräume mit vornehmlich annuellen oder biennen Pflanzen, die sich durch eine hohe Samenproduktion auszeichnen, bspw. Ackerbrachen in frühen Sukzessionsstadien, bieten Rebhühnern ein vergleichsweise großes Angebot an Samen. Die Sämereien sind zudem noch auf dem offenen Oberboden lichter Brachen oder Ruderalstandorte leicht auffindbar. Der vegetarische Anteil an der Diät der Rebhühner nimmt bis in das Adultstadium zu, in dem sie sich ganz überwiegend pflanzlich ernähren.

Charakter der Vegetation in seiner Bedeutung für das Rebhuhn

Die ökologische Einnischung einiger kleiner bis mittelgroßer Vogelarten auf vorwiegend bodengebundenen Leben führt für diese in den heutigen Agrarlandschaften Deutschlands zu Problemen. Veränderte landwirtschaftliche Modalitäten wie geringe Reihenabstände im Getreide und insgesamt homogene und dichte Bestände, die durch den modernen Pflanzenschutz, mineralische Düngung, moderne Bodenbearbeitung und Meliorationen gewährleistet werden, erschweren solchen Arten das Fortkommen auf dem Boden und damit Nahrungssuche und Feindvermeidung.

Außerdem sind Ackerrandstrukturen wie Grabenböschungen, Graswege oder Feldraine häufig vom Betriebsmitteleinsatz auf den Ackerflächen beeinflusst (e.g. Ellenberg 1992, Rew et al. 1992, Kleijn & Snoeiijing 1997, Reus et al. 2002). Verdriftung, Oberflächenabfluss und Interflow von Düngern und Pflanzenschutzmitteln können zu von wenigen nährstoffliebenden und hartnäckigen Pflanzenarten dominierten dichten Vegetationsformen auch auf den Nicht-Zielflächen führen. Dies zieht eine Verschlechterung der Lebensraumsituation für das Rebhuhn nach sich und ist damit mitverantwortlich für deren heute geringe Populationsdichten.

Beim Rebhuhn als Bodenvogel spielen sich annähernd alle Lebensäußerungen auf dem Boden ab. Standortwechsel werden in erster Linie „zu Fuß“ vollzogen. Bei Störung oder Angriff durch einen Fressfeind entziehen sie sich der Situation in der Regel durch einen zwischen 100 und 200 m weiten „Fluchtflug“. Je nach Art der Bedrohung spielt aber auch im Fluchverhalten das Fortkommen auf dem Boden in Kombination mit Deckungssuche eine große Bedeutung.

Insbesondere für die bis in die zweite Lebenswoche hinein flugunfähigen Küken hat die Mobilität auf dem Boden eine herausragende Bedeutung. In der Flucht stößt das Gesperre in alle Richtungen auseinander, um dann unter Ausnutzung ihrer Tarnfärbung regungslos auf dem Boden zu verharren. Die Wahrscheinlichkeit Fressfein-

den zu entkommen, ist in zu dichter Vegetation verringert. Bodenfeinde werden erst spät erkannt und die Flucht ist erschwert.

Der schnelle Stoffwechsel der Rebhuhnküken verlangt außerdem, dass in kurzen Zeitabständen Nahrung aufgenommen wird. Bei ihrer noch eingeschränkten Geländegängigkeit ist das leichte Erreichen der bevorzugten Arthropoden-Nahrung von herausragender Bedeutung. Ein zu hoher Raumwiderstand dichter Vegetation erhöht einerseits den Energieaufwand im Fortkommen, andererseits erschwert er die effiziente Nahrungssuche und hat damit einen negativen Einfluss auf die Überlebenschance.

Neben der reduzierten Beweglichkeit auf dem Boden diskutieren Töpfer & Stubbe (2001) als Negativum dichter Pflanzenbestände im Fall der Feldlerche (*Alauda arvensis*) auch die verringerte Möglichkeit, sich zu orientieren. Dieses Erkenntnis ist sicherlich auch auf das Rebhuhn zu übertragen. Um sein Sicherheitsbedürfnis zu befriedigen, das heißt, um auf dem Boden beweglich zu sein und das Umfeld einsehen zu können, sucht das Rebhuhn vornehmlich Vegetation auf, die dieses gewährleistet. Daraus ergibt sich für höhere Aufwüchse, dass sie „durchwanderbar“ und für niedrige Vegetation wie beispielsweise Wintersaaten von Raps, Getreide oder Grünland, dass sie „überwanderbar“ sein müssen. Eigene Kartierungen nächtlicher Schlafplätze von Rebhuhnketten mittels Wärmebildkamera bringen deren Sicherheitsbedürfnis zum Ausdruck. So werden in erster Linie Rapsschläge, Wintergetreide, Sturzäcker und lichte, schütter und niedrig bewachsene Brachen als nächtlicher Schlafplatz im Winter ausgewählt (s. Kap. IV). Hecken sowie dichte und hohe Aufwüchse auf Brachen werden eher gemieden. Mitunter wandern die Rebhühner aus der am Tage zur Nahrungssuche und als Deckung genutzten höheren Vegetation abends wieder ins offene Feld.

Dichtes Wintergetreide fällt in der Vegetationszeit für das Rebhuhn als Lebensraum aus. Regionen, in denen Kartoffel- und Spargelanbau größere Flächenanteile einnehmen, sind häufig auch durch höhere Rebhuhndichten gekennzeichnet. Auch wenn diese Feldfrüchte heute nicht mehr das Insektenangebot bzw. Wildkrautangebot vergangener Zeiten beherbergen, so sind sie strukturell noch sehr attraktiv für das Rebhuhn. Uneingeschränktes Durchlaufen ist möglich, und der offene, lockere Oberboden bietet Huderstellen.

Pflanzenbestände unterscheiden sich nicht nur in ihrer Durchwanderbarkeit sondern auch in ihrem Mikroklima. So sind etwa dichte Wintergetreide- oder Rapsbestände humider als deren Umgebung oder offenere Vegetation. Das Bestandsinnere

dichter Bestände trocknet aufgrund reduzierter Einstrahlung und verringerter Windintensität vergleichsweise langsam ab. Insbesondere die Duenenküken können in solchen Beständen schnell verklammern und schließlich der Hypothermie erliegen. Bei feuchter Witterung oder nach Regenschauern trocknen sie nur schwerlich ab und kommen immer wieder in Kontakt mit Wasser auf der Pflanzenoberfläche.

Grenzzlinien und ihre Bedeutung für das Rebhuhn

Bestandsränder haben für Rebhühner eine besondere Qualität. Dies ist insbesondere der Fall in Agrarlandschaften, in denen innerhalb der Ackerschläge kaum mehr Abwechslung in Hinblick auf die Physiognomie und Dichte der Vegetation und damit das Mikroklima gegeben ist. Diese Faktoren sowie Standorteigenschaften wie der Bodenwasser- und Bodennährstoffhaushalt sind innerhalb eines Schrages, teilweise auch über ganze Landschaftsausschnitte hinweg, hochgradig nivelliert und monoton (vgl. Berger et al. 2003). Hierin ist auch ein wichtiger Grund für die Artenverarmung der heutigen im Vergleich zu historischen Agrarlandschaften zu finden (Mühlenberg & Slowik 1997, Tillmann 2004). „Ausgeprägte“ Übergangsbiotope bestehen heute in erster Linie nur noch zwischen Schlägen in ihrem unterschiedlichen Kulturzustand bzw. mit ihren unterschiedlichen Feldfrüchten und mit Ackerrandstrukturen wie Gräben, Feldrainen oder Wegen. Dabei ist der Biotopübergang an Schlaggrenzen häufig abrupt und die Grenzlinie zum nächsten Schlag oder zur Ackerrandstruktur ausgesprochen scharf. Von einem ausgeprägten Übergangsbiotop kann hier nicht die Rede sein, eher kann von „Biotopablösung“ gesprochen werden. Der in der Wissenschaft vielfach postulierte Randeffect in seiner steigernden Wirkung auf die Artenvielfalt (vgl. Zerbe & Roweck 1991, Angelstam 1992, Risser 1995, Bock et al. 1997) kommt an solchen scharfen Grenzen nur in abgeschwächter Form zum Tragen.

Dennoch sind Ränder von Feldfruchtbeständen auch bei scharfer Grenze artenvielfältiger als das Bestandesinnere. Der kleinräumige Gradient abiotischer Faktoren vom Rand aus ins Bestandesinnere hinein - zu nennen sind hier die Licht- und Windintensität, die Luftfeuchte, die Lufttemperatur und die Temperatur und die Feuchte des Oberbodens sowie der Besiedelungsdruck im Falle einer Schlaggrenze zu einer permanenten Struktur - begründet die höhere Artenvielfalt und Populationsdichte an Ackerwildkräutern und Arthropoden. Green (1984) zeigt tendenziell für alle von ihm untersuchten Feldfruchtbestände höhere Dichten der von Rebhuhnküken bevorzugten Nahrung pflanzlichen und tierischen Ursprungs in 5 m Abstand vom Feldrand im Vergleich zu 50 m Abstand zum Feldrand. Simmering et al. (2001) stellen für intensiv

genutzte Äcker einen die α – Pflanzenartendiversität einzelner Schläge bereichernden Effekt des 2 m breiten Randes fest.

Die Ernährungsgrundlage für Rebhühner, insbesondere der Rebhuhnküken mit ihrem Bedarf an proteinreicher Arthropodennahrung, ist in den Randbereichen der Schläge in Qualität und Quantität höher. Der Aufenthalt im Übergangsbereich zweier aneinandergrenzender Strukturen der Agrarlandschaft bietet mehr Lebensraumrequisiten und Auswahlmöglichkeiten, um aktuelle Bedürfnisse kleinräumig zu befriedigen. Je nach Witterung, Tageszeit und Bedarf kann der Standort gewechselt werden. Der balzende oder der die brütende Henne betreuende Rebhahn kann im Übergang einer hohen zu einer niedrigen Feldfrucht sein Bedürfnis nach freiem Sichtfeld zur Feinderkennung befriedigen, genauso, wie er dann bei Gefahr Deckung im hohen Bestand suchen kann. Die Präferenz der Rebhühner für Randstrukturen besonders in der Brutzeit wird von vielen Autoren festgestellt (e.g. Panek 2002, Green 1984).

Grenzlindienindizes haben damit neben einer Reihe weiterer Faktoren eine große Bedeutung bei der Beschreibung der Lebensraumqualität für das Rebhuhn. Der Bedarf an Grenzlindien wird vielfach sehr statisch im Sinne von Schlaggrenzen interpretiert. Es ist jedoch ein Trugschluss anzunehmen, dass Rebhühner auf diesen Typ Grenzlindie spezialisiert sind. Vielmehr stellen Schlaggrenzlindien häufig die letzte „Attraktion“ dar, die heutige Agrarlandschaften zu bieten haben. Eine Habitatdiversität innerhalb eines Schlages mit einem heterogenen Pflanzenbestand birgt diffuse Grenzlindien und damit Übergangsbiotope in sich. Schließlich sind in natürlichen Offenhabitaten, in denen die evolutive Herkunft des Rebhuhns zu suchen ist, kaum vergleichbar klare Grenzen wie in der Agrarlandschaft zu finden. Eher bedingt die kleinskalige Biotopdiversität mit ihren meist graduellen Übergängen und damit gegebener kleinräumig hoher Dichte an beanspruchten Lebensraumrequisiten die hohe Habitatqualität.

Ökologische Aspekte der rebhuhnfreundlichen Brachegestaltung

Bekannt ist, dass frühe Stadien von Sukzessionsbrachen und Stoppelbrachen zu den beliebtesten Habitattypen des Rebhuhns zählen (Kaiser & Storch 1996; Tillmann 2006). Sukzessionsbrachen sind aber auf wüchsigen Standorten landwirtschaftlich problematisch, da dominante Unkräuter zu einer nachhaltigen Beeinträchtigung des Ackerbaus führen können. Das Ansäen von Kulturpflanzen- und autochthonen Wildpflanzenbeständen bietet eine Alternative.

Solche Ansaatbrachen unterscheiden sich von den konventionellen Feldfrüchten und sollten idealtypisch folgenden Eigenschaften besitzen, um den Lebensraum des Rebhuhns zu bereichern:

- Existenz über mehrere Jahre
 - damit bieten sie permanente Deckung und ein kontinuierliches Nahrungshabitat
 - sie sind durch störungssensible Arthropoden besiedelbar;
 - neben den angesäten Pflanzen kann eine Sukzession von Ackerwildkrautgesellschaften ablaufen;
 - Rebhühner können über mehrere Jahre eine gewohnte Struktur nutzen und den Umgang mit dieser tradieren: „Heimateffekt“ bzw. „Wohlfühleffekt“;
 - Ruhe bzw. Störungsarmut, bedingt durch Versteckmöglichkeiten, gedeckte Ausweichmöglichkeiten und ausbleibende Bearbeitungsgänge;
- Die Ernährungsgrundlage insbesondere der Rebhuhnküken wird bereichert: Arthropoden bieten sie in ihren verschiedenen Lebensstadien und Jahreszeiten Lebensraum, was neben dem ausbleibenden Pestizideinsatz Ursache für deren relativ große Vielfalt und Dichte ist;
- Ein kleinräumiges Mosaik von vegetationsfreiem Oberboden bis hin zu dichter Vegetation bietet ein Nebeneinander attraktiver Lebensraumrequisiten wie:
 - nackter Oberboden: leichtes Auffinden von Sämereien, Huderstellen, Plätze zum Sonnen;
 - dichtere Vegetation: Deckung besonders vor Greifvögeln und Nistmöglichkeiten insbesondere in dichterem Grasvegetation;
 - Heterogenität, Biotopkomplexität („Innere Grenzlinien“) machen die gesamte Stilllegungsfläche für das Rebhuhn interessant und nutzbar. Sie bietet verschiedenen Pflanzenarten Lebensraum, wobei insbesondere kurzlebige Pflanzen mit ihrer großen Samenproduktion eine wichtige Nahrungsquelle darstellen;
- Eine insgesamt schütterere, offene Vegetation ermöglicht freie Beweglichkeit auf dem Boden, freie Sicht zur Orientierung, intraspezifischen Kommunikation und Feindvermeidung.

Ansaatbrachen sollten frühe Stadien der Sukzession simulieren. Dichte und über einem Meter hohe Aufwüchse mit dem Charakter einer Hochstaudenflur bieten keine herausragende Biotopqualität für das Rebhuhn und werden nur am Rand genutzt.

Zur Brutzeit ermitteln Salek et al. (2004) die höchsten Brutpaardichten (40-90 Brutpaare / 100 ha Ödland) in Aufwüchsen mit einer durchschnittlichen Höhe von 51-65 cm.

Neben der Beschreibung der Qualität der vom Rebhuhn bevorzugten Brachflächen soll an dieser Stelle auch noch auf die aus der Sicht des Rebhuhns erforderliche Quantität eingegangen werden. Die Brutpaardichte ist in den Untersuchungen von Salek et al. (2004) positiv korreliert mit der Größe der Ruderalfläche („unmanaged wasteland“). Weiter stellen die Autoren eine positive Korrelation der Brutpaardichte mit der gesamten Ruderalfläche im Umkreis von einem Kilometer um die betrachtete Fläche fest. Das Vorkommen von Rebhühnern ist negativ korreliert mit dem Abstand zur nächsten Ödlandfläche. Zur langfristigen Stabilisierung der Rebhuhnpopulation muss die Dichte geeigneter Brachflächen kontinuierlich groß genug sein. Die Abstände zwischen solchen Flächen sollten nicht mehr als 800 m betragen. Jenny et al. (2002) belegen für ihr Untersuchungsgebiet, dass erst ab 5 % ökologisch aufgewerteter Ackerflächen in Ackerbaugebieten, ein positiver Einfluss auf die Brutvogelbestände zu verzeichnen ist; mittelfristig empfehlen sie einen Anteil von 10 %.

Je größer der Anteil geeigneter Brachflächen, desto höher sind die Brutpaardichten: die Homorange der Brutpaare nimmt mit zunehmender Habitatqualität ab, genauso, wie die Abstände zwischen den Schlafplätzen der Rebhuhnketten (Green 1984). Dies lässt darauf schließen, dass die Rebhühner in solchen Habitaten ihre Bedürfnisse kleinräumiger befriedigen können. Jenkins (1961) diskutiert außerdem die Möglichkeit, dass sich bei ausreichender Deckung höhere Rebhuhndichten etablieren, da innerartliche Konflikte und Aggressionsverhalten reduziert sind.

Angesäte Pflanzenbestände sollten Vielfalt bieten, die in intensiv genutzten Agrarlandschaften Mangelware ist. Nahrung, Nistplätze, Huderstellen, Ruhe, Deckung und damit Sicherheit müssen möglichst kleinräumig nebeneinander geboten werden.

Landwirtschaftliche Aspekte der rebhuhnfreundlichen Brachgestaltung

Neben den ökologischen Vorgaben zur Gestaltung von Brachen aus Sicht des Rebhuhns können in der heutigen Agrarlandschaft die Bedürfnisse der Landwirtschaft keinesfalls außer Acht gelassen werden. Sollen rebhuhnfreundlich begrünte Brachen im Rahmen der konjunkturellen Flächenstilllegung und als Option in Agrarumweltprogrammen breite Akzeptanz gewinnen, müssen sie aus Sicht der Landwirtschaft tragbar sein. Die Gestaltung der Brachen als anerkanntes Mittel des Naturschutzes

in der Agrarlandschaft kann sich nur durchsetzen, wenn betriebswirtschaftliche Zwänge und ackerbauliche Notwendigkeiten berücksichtigt werden. Ansaatbrachen müssen über ihre Artenzusammensetzung einen Bestand über die geplante „Laufzeit“ etablieren, der Problemunkräuter in dem Brachezeitraum unterdrückt. Das massive Auftreten von z.B. der Ackerkratzdistel (*Cirsium arvense*) führt aufgrund des Samentransportes mit der Luft auch zu Konflikten mit benachbarten Nutzflächen. Ein weiteres Problem, das in diesem Zusammenhang berücksichtigt werden muss, ist die Anreicherung des Bodens mit Diasporen von Problemunkräutern.

Die Bestandsführung ist eine Gratwanderung zwischen zu lückig und damit empfänglich für das Aufkommen von Problemunkräutern und zu dicht und damit von geringer Attraktivität für das Rebhuhn. Die Arten der Saatgutmischungen für Ansaatbrachen müssen so gewählt werden, dass die sich im Laufe der Zeit verschiebenden Dominanzverhältnisse die geforderte Lückigkeit gewährleisten. Idealtypisch sollten Brachen im Sinne des Mosaik-Zyklus-Konzeptes (von Remmert 1991 definiert für Waldgesellschaften) so angesetzt sein, dass einzelne Pflanzenarten im Laufe der Brachephase ausfallen, Lücken hinterlassen, die dann wieder von anderen aus Sicht der Landwirtschaft kontrollierbaren Kulturpflanzenarten oder Wildpflanzen geschlossen werden. Eine solche Bestandsführung ist jedoch ausgesprochen schwierig. Unterschiedliche Standortverhältnisse und nicht kontrollierbare Auflaufbedingungen durch variierende Witterung und Bodenfeuchte erlauben kaum eine pauschale Empfehlung zu Artenmischungen, die das leisten können.

Der für das Rebhuhn geforderte schütterere, heterogene Bewuchs kann also in erster Linie durch geringe Saatchichten erreicht werden. Treten Problemunkräuter auf, sind diese teilflächenspezifisch mechanisch oder chemisch zu bekämpfen. Vorgaben (Gesetze, Richtlinien, Verträge) sollten zur Steigerung der Akzeptanz solchen Maßnahmen Freiraum gewähren.

Da Brachen kleinräumig nebeneinander die vom Rebhuhn bevorzugten Lebensraumrequisiten bieten sollen, ist zu empfehlen, größere Brachen zu parzellieren. Das kann sowohl durch streifenweises Mulchen als auch durch Grubbern außerhalb der Brutzeit geschehen. Dieses Vorgehen bringt eine hohe Dichte an Übergangsbiotopen mit sich, die für das Rebhuhn äußerst attraktiv sind. Deckung, Nisthabitate und Nahrungsflächen liegen hier dicht beisammen. Ein solches Vorgehen ist besonders zu empfehlen, wenn der angesäte Bestand zu dicht aufgelaufen ist. Wenn Ansaatbrachen die Heterogenität nicht in sich bieten, dann sollte diese mechanisch hergestellt werden. Das Nebeneinander von „stehender“ Brache, gemulchter Brache

und gegrubberter Brache bietet dann die erforderliche Biotopkomplexität. Flächendeckende Bodenbearbeitung oder flächendeckendes Mulchen sollte ausbleiben, da es wieder zur Nivellierung der Biotopkomplexität führt.

Brachen, die in der Vegetationsperiode sehr dicht sind, und so der Unkrautunterdrückung nachkommen aber suboptimal für das Rebhuhn sind, sind unter Umständen im Winterhalbjahr attraktiv. Da die oberirdischen Teile einiger Pflanzenarten abgestorben oder herunter gefroren sind, bieten sie die geforderte lichte Deckung.

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Kapitel III

Fear of the dark: Night-time roosting and anti-predation behaviour in the grey partridge (*Perdix perdix* L.).

Tillmann J.E. (2009)

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Introduction

Birds potentially have some of the most complicated anti-predation behaviour (Caro, 2005). As predation is ascertained to be one of the major selective stresses determining the behaviour of animals, it might be expected that non-lethal effects of predation risks should decisively shape a bird's spatio-temporal behaviour (Lima & Dill, 1990, 1998; Tryjanowski et al., 2002; Creswell, 2008).

The grey partridge (*Perdix perdix*) is a ground dwelling *galliform* bird inhabiting open landscapes throughout its wide Eurasian range which has undergone a dramatic population decline over the last 40 years. Among others, the main causes for this trend were found to be the increase in agricultural intensity, combined with increased predation (Potts, 1980, 1986; Panek, 2005). Predation is accepted to be one of the most important factors in population dynamics of the grey partridge and for shaping its behaviour (e.g. Potts, 1986; Beani & Dessì-Fulgheri, 1998). Tapper et al. (1996) state that predation is at its most severe during laying and incubation. In contrast, predator avoidance during the 'covey season' seems more efficient, although still determining much behaviour (Tillmann, 2009).

Watson et al. (2007a) tagged 150 grey partridges with 58 % of predation involving raptors and 42 % foxes from early September - mid April. Similarly Döring & Helfrich (1986) calculated 58% of the predation mortality from October - April to raptors and 33 % to terrestrial mammals. Related to the autumn density Watson et al. (2007b) found a mortality rate of 9.5 % to raptors between autumn and spring. With some certainty raptor predation in winter is higher than predation by terrestrial predators, the opposite being the case during the breeding season.

Today, the relevant raptors in agricultural landscapes are known to be the northern goshawk (*Accipiter gentilis*), the sparrow hawk (*Accipiter nisus*), common buzzard (*Buteo buteo*), red kite (*Milvus milvus*), peregrine falcon (*Falco peregrinus*), hen harrier (*Circus cyaneus*), Montagu's harrier (*Circus pygargus*) and at night time also the eagle owl (*Bubo bubo*) and the tawny owl (*Strix aluco*) (e.g. Uttendörfer, 1952; Pulliainen, 1966; Opdam et al., 1977; Millon et al., 2002; Valkama et al., 2005; Bro et al., 2006; Park et al., 2008). As for the terrestrial predators the red fox (*Vulpes vulpes*), feral cats (*Felis catus*) and dogs (*Canis lupus familiaris*), the stone marten (*Martes foina*), polecat (*Mustela putorius*), weasel (*Mustela erminea*) and badger (*Meles meles*) are known to prey on partridges (e.g. Yocom, 1943; Pulliainen, 1966; Gatter, 2000; Baker et al., 2006; Webbon et al., 2006). Among the mentioned spe-

cies in winter-time the most important predator is usually the red fox at night and the northern goshawk during the day (e.g. Pegel, 1987; Döring & Helfrich, 1986; Glänzer et al., 1993).

Grey partridges form social groups known as coveys during the non-breeding period with a highly synchronised spatio-temporal behaviour and a lot is known about their behaviour in the daytime. Watson et al. (2007a) found that the major determinant of winter survival of the partridge is group size possibly owing to the reduction in allocation of time to vigilance, increasing the amount of time available for foraging. Furthermore, huddling in a group during cold winter nights has been shown to result in a significant reduction of the resting metabolic rate. This may consequently allow partridges to lengthen their roosting time and shorten the time spent foraging, thus assuring greater protection against cold and predators (Putaala et al., 1995). However, among ground dwelling gregarious *galliforms* the antipredator benefits of grouping seemed to be constrained to approximately 11 individuals (Williams et al., 2003; Watson et al., 2007a). The upper limit might be a result of the trade-off between beneficial effects of grouping and negative effects such as increased attractiveness to predators and intra-group competition for resources. However, this is not known for certain.

Prey species such as the grey partridge in general behave in certain ways to avoid predators, or to avoid capture when a predator is present, thereby increasing their survival rate (Cresswell, 2008). The behavioural compensation of predation risk in the grey partridges has received a great amount of attention above all in respect to the selection of the nesting site (e.g. Bro et al., 2000; Panek, 2002; Šálek et al., 2004; Wübbenhorst & Leuschner, 2006) or habitat preferences during the daytime (e.g. Döring & Helfrich, 1986; Pegel, 1987; Glänzer et al., 1993; Buner et al., 2005).

While daytime habitat preferences, especially in respect to the predatory environment in the grey partridge, are well documented investigating night-time behaviour has been neglected. So far no study has systematically analysed aspects of partridge ecology in night-time situations mostly owing to restricted observation conditions and technical restrictions. A high proportion of the grey partridge's lifetime has literally remained in the dark as in the past data collection in behavioural studies was limited to the period from sunrise to sunset.

In this study thermography was used to detect roosting partridges and to record their escape behaviour in winter at night. These results are discussed in relation to present knowledge of the diurnal habitat use and predator avoidance strategies.

Methods

To increase the probability of finding partridge coveys during the night-time surveys the study areas were chosen for viable grey partridge populations with a relatively high population density of 4 to 9 pairs / 100 ha [Tillmann, unpublished] in spring resulting in a relatively improved chance of detecting roosting coveys in the period of the wintertime study. The night-time surveys for grey partridges were conducted in 6 sites in northern Germany – two study sites in the bio-geographical region Soester Börde (approx. 51° 34' N, 8° 12' O) at 120 and 80 m a. s. l., respectively, one study site adjacent to the city of Hanover in the bio-geographical region Weser-Aller-Flachland (approx 52°31'N, 9°45'E) at 50 m a. s. l. and three study sites in the bio-geographical region Stader Geest, 20 km east of the City of Bremen (approx 53°16'N, 9°15'E) at 20 m a. s. l. The average annual temperature in the Soester Börde is 9° C and the average annual precipitation is 730 mm, in the Weser-Aller-Flachland 8.7 °C and 661 mm / a, respectively and in the Stader Geest 8.8 °C and 750 mm / a, respectively. The study sites were 200 to 920 ha in size and characterised by a percentage of at least 75 % arable land with a comparable landscape structure between study sites concerning field/forest ratio, field margin density, hedge density, average field size and crops. In this winter situation the relevant standing crops were winter rape (*Brassica napus*), winter wheat (*Triticum aestivum*), winter barley (*Hordeum vulgare*), winter rye (*Secale cereale*), triticale (x *Triticosecale*) and mustard (*Sinapis alba*). However, some stubble fields existed as well as fields without any vegetation cover. Habitat edges in these agricultural landscapes are usually sharp. Soils in all study sites are either sand dominated or shallow on calcareous subsoil and thus relatively poor with low water storage capacity and consequently relatively coarse standing crops – one of the reasons for comparatively high partridge densities in the study sites.

From the perspective of the partridge the structural and abiotic character of the 6 study sites can be described as comparable just as the predatory environment. Analysing the evolutionary framework of partridge behaviour at night the description of the principal scheme and system of the predatory environment is of prominent significance. Densities of predators were not been estimated in detail as the habitat conditions and the hunting pressure can be described as similar over the three sites. Common potential predators at night for the six sites are the red fox, stray cats, dogs running loose, from the *Mustelidae* family the stone marten, the polecat, the weasel,

and the badger and infrequently the eagle owl, the tawny owl and long-eared owl (*Asio otus*).

Relevant diurnal raptors are the goshawk, the sparrow hawk, the common buzzard, the kestrel (*Falco tinnunculus*) for chicks; rather infrequently, the peregrine falcon, red kite, the black kite (*Milvus migrans*) and Montagu's harrier. Brood and egg predators that commonly occur are the brown rat (*Rattus norvegicus*), the hedgehog (*Erinaceus europaeus*) and *Corvidae* such as the magpie (*Pica pica*), the carrion crow (*Corvus corone*) and the Eurasian jay (*Garrulus glandarius*).

For night-time detection of grey partridges and observation of their roosting and flight behaviour the handheld infrared thermal camera Raytheon model Palm IR-250 D (Raytheon Corp, Waltham, MA) was used. To record the thermal imaging from the roosting status of a covey over the escape flight until settling down again at the new roosting site for later analysis on the computer the thermal camera was connected to a video camera recorder DCR-TRV33E (Sony, Tokyo, Japan). The closer the camera the sharper the silhouette of partridges appears and their 'heat aura' is clearly contrasted to the partridge's body. With growing distance the silhouette becomes more diffuse, leading to a greater chance of confusion of other ground dwelling animals with partridges. However, the habit of roosting as coveys is exclusive for partridges in these landscapes and makes distinction from other similar sized animals simple. Small coveys of 2-4 animals roosting as a tight group might be confused with any other warm blooded animal. However, all the other medium-sized ground dwelling animals of agricultural landscapes are nocturnal and usually active in contrast to the partridge. Misinterpretation was very unlikely given that every covey was flushed.

Partridge coveys were surveyed from one hour after sunset at the earliest up to 8 hours after sunset in wintertime between 15 November 2005 and 15 February 2006.

To detect roosting coveys all available habitats and structures of the considered landscape section were scanned in detail. Relatively little scanning effort had to be invested in arable field with vegetation not higher than 15 cm. In such cases the fields could even be continuously scanned from a running vehicle and up to a distance of 250 m. Usually, however, the car was left every 100 m at topographically exposed locations or locations with an open panoramic vision to then scan in detail for roosting coveys. Arable fields with higher vegetation – i.e. oilseed radish, mustard, set aside fields or in some cases rape - had to be entered on foot as well as hedges, field margins or bush groups having to be thermographically scanned from a closer distance to guarantee a complete detection of present coveys.

Once a covey had been detected it was directly approached as silently as possible at a slow and steady walking pace of ca. 0.5 m/s in a standardised manner as a prey's response towards a potential predator is expected to be influenced by the predators' speed and direction of approach (Burger & Gochfeld, 1990; Stankowich & Blumstein, 2005). Starting with a distance to the covey of ca. 100 m and drawing closer to the covey the video camera recorder was turned on to record the roosting and flight behaviour. To keep the escape behaviour of partridge coveys comparable to a high degree the process of approaching the covey was standardised as far as possible. Usually the covey was approached instantaneously after detection, in a perpendicular line to the road from which the covey had been detected.

Approaching a covey more than once per night was easily avoided as the new roosting site of the covey was recorded and marked on a map. Similarly, approaching coveys a second time between two observation nights was avoided by choosing different sections of the study area. Between two observation nights in one study area there was a time delay of at least 7 days (as described in Tillmann, 2008). However, monitoring the behaviour of a covey a second time could not be absolutely avoided given an average home range size in winter of 14 ha according to Buner et al. (2005), or 11.06 ha according to Döring & Helfrich (1986).

The spatial arrangement of a roosting covey and the number of individuals per covey was determined from the thermographic records on the computer. The grouping character of a roosting covey was classified as follows:

- 0) = all individuals sitting solitarily
- 1) < 50% grouped with physical contact
- 2) > 50% grouped with physical contact
- 3) = all individuals with physical contact

Additionally, for each covey the roosting 'subunits' of individuals with physical contact were registered and the percentage of individuals having physical contact with at least one other individual was determined.

The flight initiation distance (FID) – as the distance between the approaching observer and the covey when starting the escape flight – could be easily measured with a tape measure in a situation with snow cover. Otherwise, after the whole complex of escape behaviour had been recorded the roosting site, indicated by depressions in the vegetation and faecal droplets, was searched for with a torch and then the FID was measured.

As for the escape behaviour itself some prominent characteristics were identified in a pilot study and accordingly registered in the present study. The considered variables and parameters of the escape flight were:

1. initial flight character
 1. direct take-off of all individuals
 2. direct take-off – a small number of birds run a few steps before take-off
 3. all individuals run at least 5 m before take-off
 4. all individuals run away – no take-off
2. call intensity during escape flight
 1. all individuals are silent
 2. single individuals calling (less than 4 calls)
 3. 'concert' (>>4 calls)
3. defecation when flushed
 1. no defecation
 2. each individual defecates ca. once
 3. each individual defecates more than once
4. initial escape in a clockwise direction relating to the line of approach
5. final escape direction / direction of the landing position clockwise relating to the line of approach
6. pattern / character of the flight line (see Figure 6)
7. duration of the escape flight [s]
9. escape flight distance [m]
8. escape flight distance as straight line between the original roosting site and the new roosting site [m]

The considered environmental conditions are:

1. time (no. of minutes after sunset)
2. roosting site characteristics:
 - (a) crop type (1 = winter barley, 2 = winter rape, 3 = winter wheat; 4 = stubble [corn or maize], 5 = winter rye / triticale, 6 = field grass / grass fallow, 7 = mustard / oilseed radish, 8 = recently ploughed field)
 - (b) crop character (1 = dense / felted, 2 = heterogeneous / sparse, 3 = open soil surface)
 - (c) vegetation cover [%]
 - (d) vegetation height [cm]

- (e) soil condition (1 = soaked, 2 = moist, unfreezing, 3 = frozen)
- (f) local topography of roosting site (1 = plain, 2 = crest, 3 = shoulder, 4 = depression)
- (g) hillside situation (inclination in °)
- (h) snow cover [%]
- (i) snow depth [cm]
- (j) distance of the roosting site to the closest other structure differing 10 cm in height (e.g. hedge, grass strip, farm track, herbaceous or grassy vegetation associated with a ditch or watercourse, adjacent crop etc.)

3. air temperature [°C]

4. wind force (1 = calm to light air, 2 = light to gentle breeze, 3 = moderate to fresh breeze, 4 = strong breeze to near gale) on the basis of the Beaufort wind scale

5. precipitation

- (a) shower (short downpour with large raindrops)
- (b) drizzle (the finest formation of droplets)
- (c) steady rain (long, steady rain with medium-sized drops)
- (d) drizzle (small drops over a longer period of time)
- (e) slight snowfall
- (f) average snowfall

6. cloud amount [%]

7. light intensity (1–3)

8. moon phase (100 % = full moon)

The assumption of normality was tested for continuous variables with the Kolmogorov-Smirnov-Test; for discrete variables the assumption of normality was tested with the Chi-Square test. When the assumption of normality was satisfied the distribution of the variables was characterised by the arithmetic mean (mean) and the standard error of the arithmetic mean (SE), otherwise it was characterised by the median and the 25th and respectively the 75th percentile (p_{25} and p_{75}).

To analyse the strength of the relationship between two variables the Kendall-Tau-b test was used for non-parametric variables and Pearson Product Moment Correlations were used for parametric variables. For calculating multiple logistic regres-

sions in SAS 9.1.3. (2007) the procedure 'logistic' was used; for all other analyses SPSS 15.0 (2007) was used.

Results

Roosting behaviour

The use of a thermal camera proved to be a very practicable device for surveying partridge coveys in open landscapes at night. On average a 5 h survey was conducted per night during which approximately between 150 and 400 ha could be scanned for roosting partridges. In open flat habitats thermography enables scanning for partridges up to a distance of 250 metres. As the camera detects temperature differences its use is optimal in the combination of winter and night time.

The night-time surveys detected between 0 and 8 partridge coveys. In total 640 partridges in 102 coveys were found in 85 scanning hours. Not every detected covey and its behaviour could be analysed concerning all considered behavioural traits, since recording conditions could be unfavourable due to weather conditions, local topography or obstructions, such as hedgerows or buildings, that obscured parts of the escape behaviour.

As depicted in Figure 1, in 83 out of 96 coveys the majority of partridges roosted in direct physical contact with other individuals.

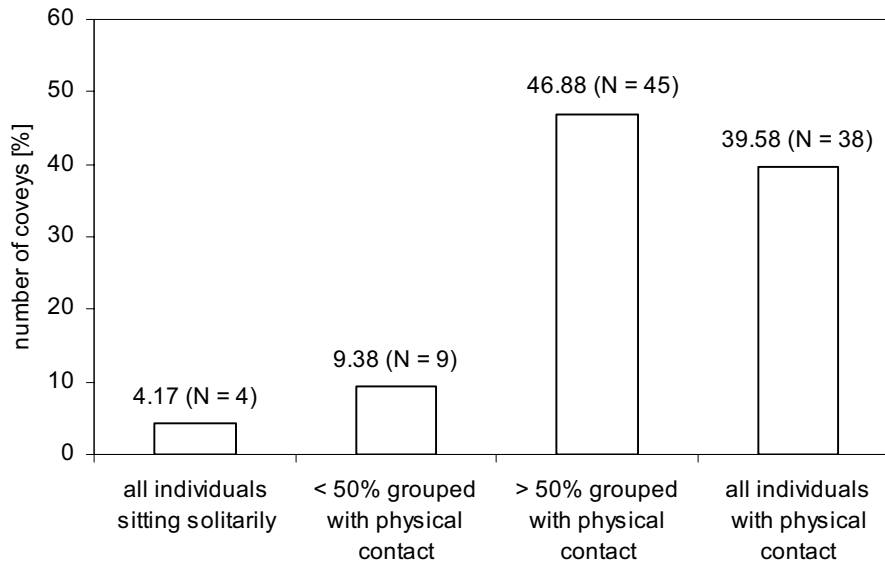


Figure 1. Grouping character of roosting grey partridges at night (number of coveys indicated in brackets).

81.75 % ($N = 401$) of the 537 individual partridges in coveys ≥ 2 individuals had physical contact with at least one other individual. Consequently 18.24 % ($N = 98$) roosted within the covey without physical contact. The proportion of partridges with physical contact with at least one other individual for 71 coveys where it was measurable was significantly negatively correlated with the moon phase (Spearman-Rho $r = -0.431^{**}$, $p = 0.000$) and temperature (Spearman-Rho $r = -0.256^*$, $p = 0.031$). A significant positive correlation of the 'cuddle up' proportion was found with the time after sunset (Spearman-Rho $r = 0.273^*$, $p = 0.021$) and the snow depth (Spearman-Rho $r = 0.270^*$, $p = 0.023$), whereas the 'cuddle up' proportion was neither related to covey size, cloud amount, the distance to the field margin, the slope, the crop height nor to the crop cover. No significant relation of the 'cuddle up' degree and the ordinal parameters wind force, precipitation, crop type, crop character or soil condition was found using the Kruskal Wallis Test.

Roosting individuals of one covey usually spread themselves over an area no larger than 2.5 m². If not sitting tightly together individual partridges are usually not further than 60 cm away from each other.

Approaching the pairing season partridges often roost in a rather scattered manner a few days before the final break up and dispersal (compare Figure 2a).

Considering only coveys with ≥ 3 individuals ($N = 72$) the subgroup affiliation of 499 individual partridges could be measured. In the case of 38 % most individual partridges ($N = 192$) of those coveys were 'grouped' in subunits of single or two individuals. Diverse variants of roosting formation in partridge coveys are given in the thermographic pictures of Figure 2 a-i.

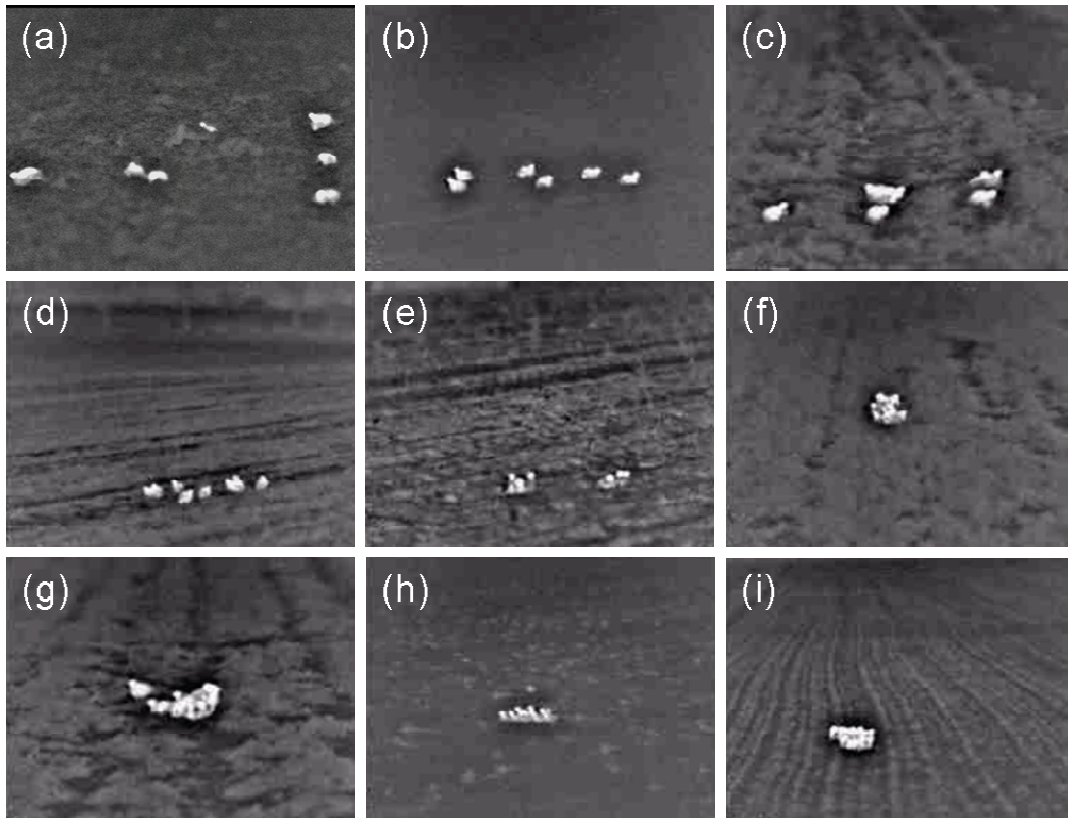


Figure 2. Different roosting formations within grey partridge coveys (a-i).

17 observed partridge 'pairs' had physical contact without exception. In many cases the pairs settled with their heads pointing outwards in the opposite direction (Figure 3).



Figure 3. Examples of thermographic pictures of pairs showing each facing a different direction.

Individuals of coveys with all partridges roosting in physical contact to each other usually face outwards. Partridge coveys generally roosted in open arable fields. The distance of the roosting location to the next different structure, defined as field margin or vegetation, at least 10 cm different in height than at the roosting site, ranged between 9 and 150 m (median = 60; $p_{25} = 36.78$, $p_{75} = 100$). A significant relationship of the distance of the roosting site to the field margin was found with the light condition (Kruskal-Wallis-Test, $df = 22$, $p = 0.008$) and wind force (Kruskal-Wallis-Test, $df = 26$, $p = 0.015$). Checking this result with the Mann-Whitney-U- test it could be proved that the darker the light the greater the distance is to the margin (Mann-Whitney-U test, $Z = -2.770$, $p = 0.006$). Concerning the wind strength no clear result was found. By means of a pairwise comparison of the 4 classes of wind strength only a significant difference between class 3 (= moderate to fresh breeze), with a median distance to the margin of 70 m and class 4 (= strong breeze to near gale), with a median distance to the margin of 45 m, was found (Mann-Whitney-U test, $Z = -2.224$, $p = 0.026$).

None of the 102 detected coveys roosted in the direct vicinity of field margins, any type of road, gardens, woods, ditches or underneath bushes, in hedges or in fields with crops and set aside vegetation higher than 12 cm, even though available. All coveys roosted on arable fields, none on permanent grassland (Figure 4). Considering the availability of crops in the research sites a preference for rape was found – where stubble with weeds was available these fields were also preferred over other habitat structures.

The vegetation height of the crops at the roosting site ranged from bare soil with or without a sparse flora to 12 cm (compare Figure 4). Thus, partridges had the chance to oversee the surroundings in most cases without having to stretch their neck. The vegetation cover at the roosting site ranged between 0 and 95 % depend-

ing on the crop (Figure 4). If there was bare soil between the crops these microhabitats were usually favoured as individual roosting sites instead of roosting on the plants, this being typical in rape but also in cereal fields.

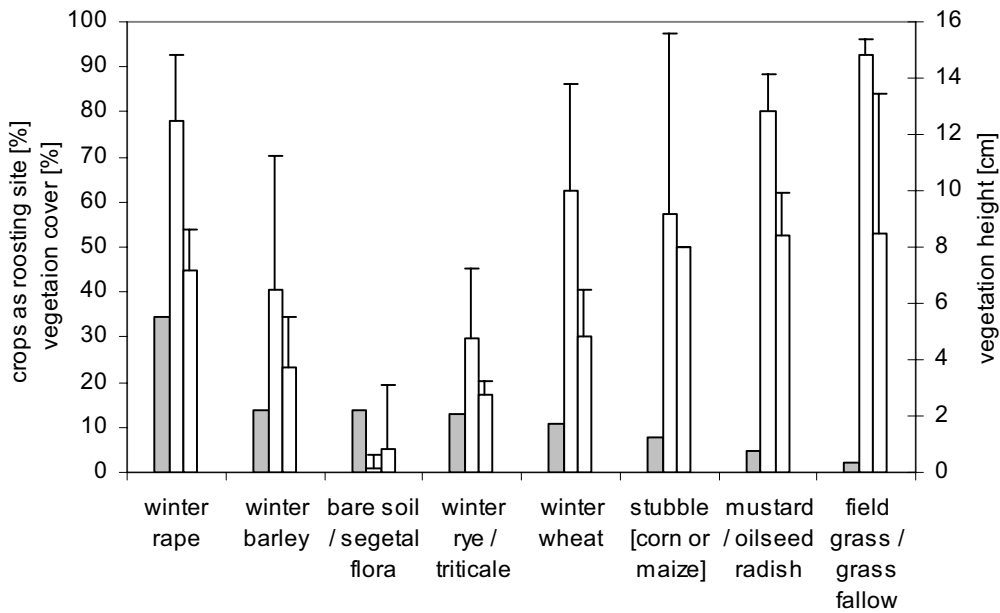


Figure 4. Proportion of crops as roosting site for partridge coveys ($N = 102$) indicated as grey column and the corresponding mean vegetation cover (left, white column) and mean vegetation height (right white column) at the roosting sites (white columns with standard deviation indicated).

As for the local topography at the roosting site 59.41 % ($N = 60$) of the coveys roosted on raised areas (crests), 30.69 % ($N = 31$) in a flat location, 9.9 % ($N = 10$) on a shoulder between 1° and 4° inclination and no covey roosted in depressions. The intensity of relief in the study areas was relatively low, ranging between 0.5 and 4 m / km².

In the case of rape, and to a limited extent also in winter grain around individual roosting sites, beak marks gave evidence of feeding activity at the roosting site probably at dusk and/or dawn. During the observations that were conducted between 68 and 443 min after sunset (mean = 234.78, SE = 8.82) feeding activity or any active comfort behaviour was never registered. Partridge coveys usually roosted motionlessly with no visual interaction between individuals and in absolute silence. A

change of roosting location at night was never observed without an obvious disturbance.

Escape behaviour

FID ranged between 7 and 70 m (median = 20; $p_{25} = 15$, $p_{75} = 29.25$). A significant correlation of the FID was found with covey size (Spearman-Rho $r = 2.68^{**}$, $p = 0.007$), with the distance of the roosting site to the nearest different structure (Spearman-Rho $r = 0.259^{**}$, $p = 0.009$), with the cloud cover (Spearman-Rho $r = -0.380^{**}$, $p = 0.000$) and with the intercorrelated complex of snow cover (Spearman-Rho $r = 0.422^{**}$, $p = 0.000$), snow depth (Spearman-Rho $r = 0.367^{**}$, $p = 0.000$) and temperature (Spearman-Rho $r = -0.335^{**}$, $p = 0.001$).

Using the Kruskal-Wallis-Test for a relationship of the FID with the ordinal variables a significant relationship with the light conditions was found that could prove that the better the light the further the FID is (Mann-Whitney-U test, $Z = -4.122$, $p = 0.000$).

In respect to the initial character of the flight in 83.84 % ($N = 83$ out of 99) the disturbed coveys started their escape flight almost synchronously and directly from the roosting position. The start was very surprising and explosive.

Considering the ordinal environmental variables a significant association of the initial character of the flight with crop character was found - the probability that partridges ran a few steps before taking off increased the sparser the vegetation was (Pearson chi-square $df = 2$, $p = 0.031$; Kendall-Tau-b = 0.250). In a multiple logistic regression no significant relation of the initial flight character to any of the considered metric variables was found.

Flushed grey partridge coveys started the escape flight more or less exactly in the antipodal direction of the observer approach direction. Clockwise, considering the observers approach direction in 95.75 % ($N = 90$ out of 94) partridge coveys started their escape flight between 11:00 and 13:00 (see Figure 5). By contrast the landing position in relation to the line of approach was much wider as the escape flight is typically bow-shaped - it ranged from 06:00 to 16:00.

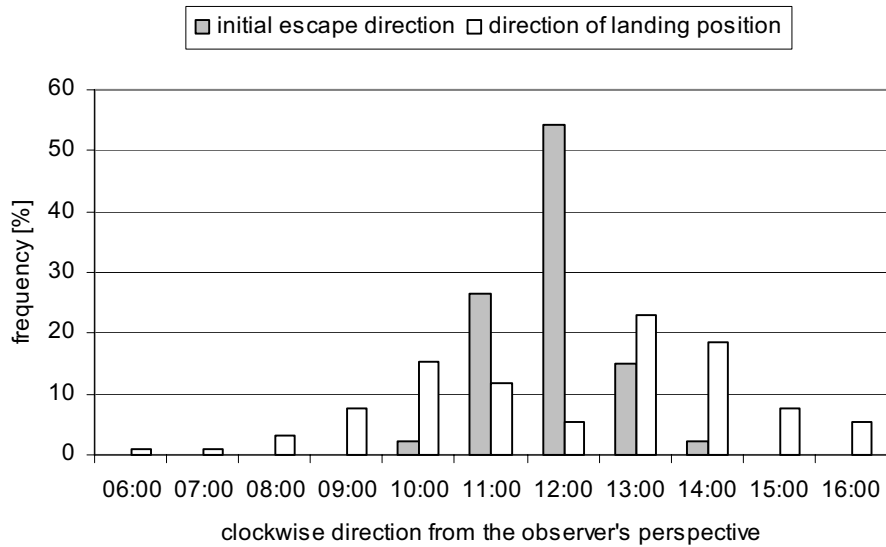


Figure 5. Clockwise initial escape direction and direction of the landing position relating to the approach line.

The escape flight itself could be classified as seen in Figure 6. During the escape flight, partridges stayed together in the covey taking the same route. If no obstructions had to be overflowed the flying altitude ranged between an estimated 2 and 7 m. It was never observed that partridges collided with obstructions such as trees, bushes or buildings during their escape flight. They were able to fly over, for example an avenue with 30 m high hybrid poplar trees (*Populus x canadensis*) or 10 m high buildings with ease. Occasionally it appeared that the partridge coveys were geared to avenues or hedges on their way to a new roosting location. Altogether partridges seem to be confident concerning orientation at night. Just before landing in all observations partridges swung sideways or almost in the direction they had come from to then decelerate by increasing their altitude slightly, finally falling by flagging steeply in a rather ungraceful manner. It never occurred that partridges took flight in a straight line indicated as (1) in Figure 6. In 66.67 % ($N = 62$) the escape flight could be characterised as type (4), in 18.28 % ($N = 17$) as type (2) and in 15.05 % ($N = 13$) as type (3), respectively.

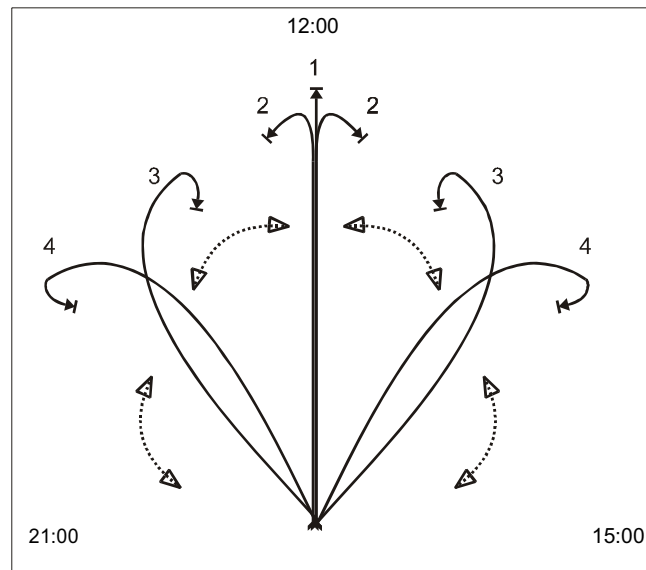


Figure 6. Schematic flight line of partridge coveys when flushed.

After landing, partridges immediately started to reorganise themselves in a new roosting position, whereas they again aligned with each other in a walking or running manner. This process seemed to be independent of the initial disturbance – no further tendency to proceed distancing themselves from the predator stimulus on the ground could be registered. This resettling process until roosting again in a motionless manner usually took less than 30 s.

In 74 % of the flushed coveys partridges remained silent during the escape flight and the only sound made was the flapping of the wings. Due to the instantaneous, explosive and synchronous take-off of all individuals in a covey the approaching observer - even though anticipating the flush – was still always surprised. In 26 % partridges uttered calls during the escape flight (Figure 7).

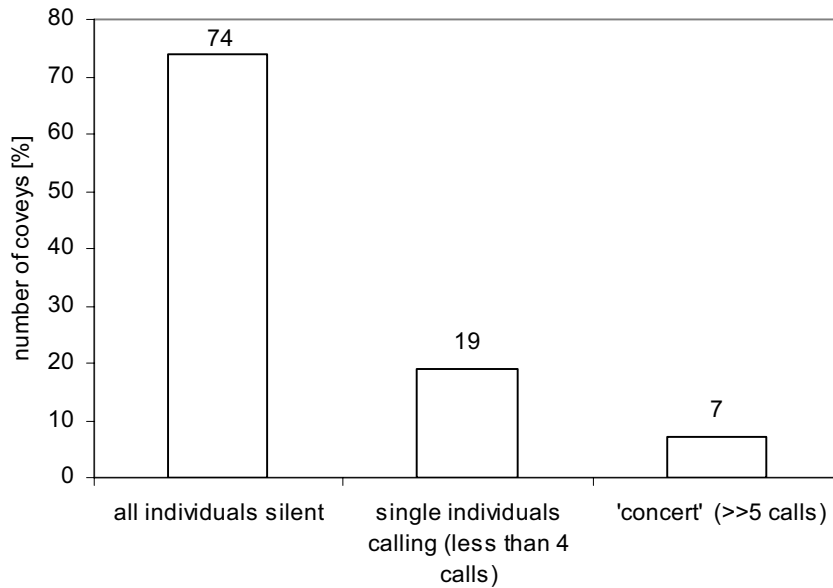


Figure 7. Call intensity during escape flight of 100 flushed coveys.

Call intensity was weakly negative related to the light intensity (Pearson chi-square $df = 4$, $p = 0.049$; Kendall-Tau-b = -0.243). For a multiple logistic regression the three original classes of call intensity have been divided into either 'all individuals silent' and 'occurrence of calls' during the escape flight. No significant relation of the behavioural variable 'call' to any of the considered variables was found.

The duration of the escape flight from being flushed until settling at the new roosting site ranged between 7 and 25 s (mean = 14.27 s; SE = 0.39). The duration of the escape flight was correlated with the covey size (Spearman-Rho $r = 0.269^{**}$, $p = 0.008$) and also weakly with the time elapsing after sunset (Spearman-Rho $r = 0.207^{***}$, $p = 0.045$).

The straight-line of the escape flight distance in 98 flushed coveys could be estimated analysing the thermographic records on the computer with the aid of a map on a scale of 1:5000. The median distance was 120 m ($p_{25} = 90$, $p_{75} = 150$). As partridges typically fly in a bow this distance does not exactly reflect the distance covered. To calculate an approximation measure to the real flight distance the flight duration in seconds and the flight speed of 40 km/h as described by Harrison (1931) as lower border of the flight speed in the grey partridge was consulted. According to this calculation the flight distance ranged between 77.78 and 277.78 m (median = 155.56; $p_{25} = 122.22$, $p_{75} = 188.89$). In contrast to the straight-line of escape flight in

this calculation the flight distance differed significantly between pairs and coveys (Mann-Whitney-U test, $Z = -3.304$, $p = 0.001$) with a median of 133.33 m ($p_{25} = 108.33$, $p_{75} = 144.44$) vs. 155.56 m ($p_{25} = 133.33$, $p_{75} = 188.89$).

Towards the end of winter (i.e. towards mid-February), approaching the breeding season, the frequency of pair observation increased. A total of 21 pairs were observed. Even though these pairs could not be sexed at night it is assumed that those pairs consist of a cock and a hen and therefore potentially have a specific social and also behavioural quality compared to coveys with more than two individuals. No significant differences between pairs and coveys ≥ 3 individuals could be found considering the various variables concerning roosting habitat choice. In contrast, in the complexity of the surveyed behavioural traits the FID was significantly higher with a median of 21.5 m vs. 15 m in coveys > 2 individuals compared to pairs (Mann-Whitney-U test, $Z = -2.297$, $p = 0.22$). Moreover, the duration of the escape flight and the length of the escape flight was with a median of 14 s vs. 12 s higher in coveys than in pairs (Mann-Whitney-U test, $Z = -3.304$, $p = 0.001$). The call intensity during the initial stage of escape flight was higher in pairs than in coveys (Mann-Whitney-U test, $Z = -3.119$, $p = 0.002$).

Discussion

Grey partridge coveys have been observed to leave their foraging habitat in the evening to then fly up to several hundred metres often to open fields as this predator avoidance routine is considered to break the scent trail which could lead terrestrial predators to the roosting covey (Yocom, 1943; Potts, 1986; Tillmann, 2006). Until the present study this was the last behaviour documented before nightfall. The relocation indicates a switch in the anti-predator strategy between day and night. In this study it was shown that at night grey partridge coveys avoid field boundaries, edge structures such as hedges, grassland and higher vegetation. On average the roosting site was located 60 m away from the field margin in lower and sparser vegetation compared to other available habitats with an unrestricted all-round view in most cases in topographically exposed locations. For such roosting locations a different predatory quality and quantity can be expected compared to higher vegetation and the areas at the edge of fields that are known to be important habitats for the relevant predominantly nocturnal predators (e.g. Harris & Woollard, 2005) and other nocturnal mammals as potential disturbers of roosting partridges. Increased nest predation rates in

various bird species along edges indicate the elevated predatory pressure on edge structures (for respective publications see Tryjanowski, 2000; Evans, 2004) and support the ecological trap hypothesis. As ascertained in this study partridges indeed attributed a higher predation risk to such structures as they not only avoided roosting close to them, as described above, but also kept the distance of the roost to the field boundary greater the darker the night was – an adaptive consequence of unfavourable conditions to visually detect approaching predators and of increased predator activity during darker nights (e.g. Shapira et al., 2008). Accordingly, Beauchamp & McNeil (2003) find an increased vigilance level in foraging greater flamingos (*Phoenicopterus ruber*) during darker nights, indicating a higher level of fear due to limited visibility of predators.

While at night terrestrial predators dominate, during the daytime the risk of being attacked by a raptor is higher. Partridges tend to stay in or close to hiding cover during the daytime (see Šálek et al., 2004), a behaviour contrasting to the night-time spatial behaviour found in this study. Glänzer et al. (1993), for example, describe a rather strict bond of partridges to cover during the daytime in areas with a higher goshawk abundance compared to partridge habitats without goshawks where partridges are more frequently found in open fields. Partridges are easily descried by the diurnal set of raptors on open arable fields in winter; particularly on the symmetric rows in winter grains every irregularity attracts the attention of raptors. During the daytime partridges therefore stay close to hiding cover to keep the escape route short, thus decreasing the risk of being preyed upon by a raptor.

The behaviour of the nocturnal terrestrial predators in combination with the predation behaviour of the diurnal raptors creates a predictable spatio-temporal pattern of predation risk for the grey partridge. In various studies the spatial pattern of predator avoidance strategies is described for various predator-prey interaction sets (e.g. Thomson et al., 2006). However, the temporal component in spatial avoidance strategies of predation risks has been broadly neglected probably because almost always only two interactors were analysed in the predator-prey systems. In hardly any investigation have the effects of circadian shifts in the predatory environment on a prey species behaviour been described in detail.

In this study evidence is found that the grey partridge not only perceives a spatial “predation risk landscape” (sensu Thomson et al., 2006) but moreover perceives a circadian ‘predation schedule’ attributing certain landscape features to changing predation risks in the course of a day. In consideration of its needs besides predator

avoidance the grey partridge shapes its spatio-temporal behaviour as a negative pattern to the shift in predation pressure over space and time.

Considering the circadian shift of the predatory quality the functionality of vegetation alternates from protective during the day-time to obstructive at night (compare Lazarus & Symonds, 1992). Upon an attack by a terrestrial predator any vegetation could hamper the partridge's strategy to explosively flush, the common way to flee at night according to the observations during this study. Their habit of roosting in relatively open cover, because of being able to quickly take wing, are great advantages in escaping night predation (Yocom, 1943). Moreover, roosting in open arable fields with low, sparse vegetation has the advantage that predators that frequently search for prey on fields, in particular the red fox, are detected early enough so as to successfully escape from them. Even though the as silent as possible approach of an observer is not comparable to that of a stealthy fox the flight initiation distance of on average 22.8 m indicates an early and efficient predator stimulus reception in roosting partridge coveys. The predator detection at night is obviously not limited compared to the daytime situation in which Yocom (1943) estimates the FID to be approximately 19 m.

Interestingly, the FID increases with an increasing distance of the roosting site from the field boundary. As the observer approaches the roosting covey in a direct line it is assumed that the partridges roosting further away from the field boundary have a longer time to decide if the disturber is a threat, therefore it being worth their while in investing in an escape flight and flushing earlier. This is in accordance with escape theory that states that flight initiation distance increases with directness of a predator's approach (Cooper & Whiting, 2007), but furthermore amends the theory: the longer the direct approach, the bigger the FID.

The finding that dense vegetation and vegetation higher than 12 cm was avoided supports the hypothesis that such vegetation obscures the partridge's visual field more, making it feel insecure. The increasing FID with better light conditions, as found in this study, indicates the prominence of visual detection of predators in partridges even at night. Kassinis [pers. communication] observed in another *galliform*, the chukar (*Alectoris chukar*), a preference for roosts in the middle of arable fields in the population living in the arable plains. Further, in contrast, the population living on higher ground where the terrain is rugged and bushy roosts on large rocks at the edge of the slope overlooking a large territory, giving them an early warning advantage to flee if danger comes close. In accordance with the 'many-eyes' hypothesis

(Lima, 1995) the more individuals per covey the bigger was the FID, suggesting that the collective detection is enhanced when more eyes scan the environment for predators. Groups are known to detect predators more efficiently and can also have the advantage of predation risk dilution and confusion of attacking predators (e.g. Elgar, 1998; Williams et al., 2003; Watson et al., 2007a). Individuals in groups are known to be able to reduce their vigilance levels significantly without compromising their ability to detect predators, thus allocating more time to other needs than predator avoidance. Usually roosting partridges in a group point their heads outwards so that the sensory apparatus of each individual can efficiently constitute to the covey's predator detection. With lower temperatures partridges were found to form tighter groupings reducing individual surface area and therefore individual heat loss (see also Putaala, 1995; Lu & Ciren, 2002; Hiller & Guthery, 2005). The coveys roosted also tighter together the more time had elapsed after sunset which might be explained by falling temperatures in the course of a night indicating – even though never observed - some adjustment in roosting formation according to changing environmental conditions over night. Likewise, partridges were ascertained to roost in tighter groupings on darker nights. I hypothesise that the efficiency of visual detection decreases with deteriorating light conditions - confirmed by a decreasing FID - and partridges draw closer together, fearing such an insecure situation and rather trusting in anti-predatory measures such as the explosive, confusing flush in combination with defensive defecation as described by Tillmann (2008).

However, partridges obviously prefer to roost in smaller subunits within one covey, potentially because the visual field for detecting predators might be larger compared to a tight grouping with individuals roosting in the centre of the covey, possibly having an obstructed view. Further investigations are needed here to clarify the cause for this behaviour as it also might be triggered by thermoregulatory reasons or social interactions. The roosting site selection seems to be to a certain extent a trade off between predator avoidance and energy economy. The trend was for partridges to roost closer to boundary structures giving wind shelter the stronger the wind was. The wind chill factor on the open field is expected to be somewhat higher than in the direct vicinity of higher vegetation such as a hedge. Therefore, it can be assumed that a roosting location in the wind shade of higher vegetation has energetic advantages. However, considering the mild winters in the study and given the partridge's morphology and plumage being well adapted, as it evolved in rather open landscapes with high wind force and low temperatures in winter, the energetic ad-

vantage is expected to be rather marginal. Therefore, the opportunity costs of avoiding predators by roosting in the open field are considered marginal.

In the investigated night-time situation no effects of group size on the habitat choice could be found. This result contrasts with the day-time behaviour as found by Watson et al. (2007a) describing larger coveys as using tall vegetation less than smaller groups owing to an improved predator detection in larger groups.

From a distance all partridge coveys detected in this study at night-time were resting motionless in a crouched manner until the observer was so close that partridges started their escape behaviour. The vigilant upright posture commonly observed in partridges during the day-time (Beani & Dessi-Fulgheri, 1998; Watson et al., 2007a) was only observed just before take-off. According to Watson et al. (2007a) vigilant behaviour can potentially increase predation risk in a cryptic animal such as the partridge because it increases exposure time and conspicuousness. Comparing day-time vigilance and night-time anti-predation behaviour the costs of day-time vigilance are obviously saved at night as this behaviour seems to be unnecessary or disadvantageous when roosting far enough away from areas with the highest predation risk. This finding corresponds to that of Suhonen et al. (1994) and Schultz & Noë (2002) who state that avoidance of predators also reduces the importance of vigilance. Usually in predator areas an increased level of vigilance and a higher predation risk reduce overall fitness. The strategic selection of roosting sites with a relatively low predation and disturbance risk ensures a quiet energy-saving and relaxing sleep for effective reactivity and vigilance performance the following day. Those coveys not disturbed or attacked are able to allocate more time to relaxing sleep in relation to vigilance and active predator avoidance behaviour, thus saving energy, having an additional delayed selective advantage through increased overall fitness especially the following day. During the night-time observations only in two instances a brown hare (*Lepus europaeus*) ran into a roosting covey and caused it to flush. It is expected that partridge coveys rather seldom are forced to flee at night due to their strategic choice of the roosting site. For this reason and given that the observations took place in the first half of the night the behavioural parameters such as the FID or flight distance are expected to be rather unbiased by an earlier disturbance.

If nevertheless a predator approaches, the decision to flee is based on a balance of risks and costs while the partridges remain cryptic (e.g. Cooper & Frederick, 2007). The partridge must simultaneously assess the probability of being detected or being captured if detected, making the best escape decision in response to the

predator specific attack strategy (sensu Broom & Ruxton, 2005). In 95 % of the approached coveys all individuals flushed more or less synchronously. This high percentage contrasts to daytime escape behaviour when partridges often, as first choice, try to run out of the reach of a detected terrestrial disturbance to stay out of the sight of raptors, thus profiting from the cryptic ground dwelling behaviour and their camouflage plumage. Diurnal raptors such as the goshawk or the peregrine falcon usually attack their prey in the air making escape flights risky. Therefore, partridges usually crouch or run for cover if a raptor is detected (compare Lu & Ciren, 2002). At night potential aerial predators such as the eagle owl usually do not attack flying prey. Thus, flying at night seems to be a relatively save option when avoiding nocturnal terrestrial predators, the first choice as escape movement as found in this study. However, a further reason for preferentially flying away at night might be hampered orientation and poor visibility on the ground. During the escape flight, in 26 % of the flushed coveys partridges uttered a series of agitated calls especially during the initial stage of flush – never during the second half of the escape flight. Yocom's (1943) expression "confusion chorus" for a similar observation in the grey partridge is also applicable to my findings especially given the increased call intensity with poor visibility. Partridges flush in antipodal direction to the approacher to then fly in a bow, finally diverging right or left before landing probably to overfly the new roosting site to scan for predators and to scan the habitat structure. The escape flight length as a straight line between disturber and the new roosting location averaged 120 m and as a trade-off between predator avoidance and energetic costs seemed to make the partridges confident as no agitated behaviour towards the initial reason to flee could be identified and partridges again settled down calmly at the new roosting site.

Anti-predatory behaviour in the grey partridge is found to be generally effective in winter and thus the predation rate is relatively low compared to the severe predation on partridges during the breeding season (Tapper et al., 1996). In this study for the first time night-time roosting behaviour of the grey partridge with special regard to its efficient strategy to avoid and escape from predators was documented and discussed.

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Kapitel IV

**An ethological perspective on defecation as
integral part of anti-predatory behaviour in the
grey partridge (*Perdix perdix* L.) at night.**

Tillmann J.E. 2009

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Introduction

While foraging in birds has been a major focus of behavioural research, its obligate partner, defecation, has been comparatively neglected and there are many unresolved issues especially with regard to defecation in behavioural complexes other than depositing metabolic waste. For example the removal of faecal sacs produced by nestlings is common behaviour in many species of birds, yet it is poorly understood. The possible benefits have been explained in terms of nest hygiene (Thompson 1935; Nisbet 1983; Spencer 2005) or reduction in conspicuousness of the nest site to predators (Petit et al. 1989). In addition, in many cases parent birds eat the faecal sacs, considered not just as an alternative strategy to removal but also to provide nutrients and energy as well as to recycle water (McGowan 1995; Dell’Omo 1998).

Defecation is a well known reaction of birds being under predatory pressure. Every bird bander has experienced this behaviour while handling birds (e.g. described by Ricklefs 1977 for various passerine birds). Various bird species have been observed during the day time to abruptly defecate when surprisingly flushed, being in a potentially threatening situation from the birds` perspective; e.g. herons (*Ardeidae*) (Mester 1976), bobwhite quail (*Colinus virginianus*) (Fatora 1968), greylag goose (*Anser anser*) (Lorenz 1964) or great bustard (*Otis tarda*) that excrete hydrous, malodorous caecal faeces while uttering fright calls upon being flushed (Glutz von Blotzheim and Bauer 1994a).

Defecation in the context of predator avoidance has been described for various bird species. For further bird species a direct and well targeted use of faecal material in the context of anti-predator behaviour has been evidenced to be effective. Nestling hoopoes (*Upupa epops*) for instance squirt faeces towards predators as a defensive strategy (Glutz von Blotzheim and Bauer 1994b). As reviewed by Mester (1976) the Houbara bustard (*Chlamydotis undulata*) spreads its flight feathers of tail like a fan on attacking falcons, so as to then eject faeces towards the aggressor. The fieldfare (*Turdus pilaris*) actively uses its faeces in its aggressive nest defence (Löhrl 1983; Hogstad 2004). Mester (1976) describes a similar behaviour for mistle thrushes (*Turdus viscivorus*) and song thrushes (*Turdus philomelos*) when protecting their brood. When attacking potential predators of their brood the common tern (*Sterna hirundo*) habitually defecates at the lowest point of its dives often hitting the predators (Nisbet 1983). This behaviour is also to be observed in other terns (*Sternidae*).

Waterfowl (*Anatidae*) are known to defecate on their nests and eggs, respectively when flushed. This protective mechanism appears to repel nest predators like foxes, rats and *Mustelidae*. In his experimental approach Swennen (1968) found that even hungry “classical” egg predators like the ferret (*Mustela putorius f. furo*) and rats (*Rattus norvegicus*) avoid eggs of the northern shoveler (*Anas clypeata*) and common eider (*Somateria mollissima*) treated with their “flight” faeces even at a high dilution rate. Protective defecation over the clutch has also been described for the snipe (*Gallinago gallinago*) and great snipe (*Gallinago media*) (Müller and Königstedt 1990). Mester (1976) hypothesises a repulsive, nauseous value of faeces, whereas this effect was selected as a secondary benefit in deterring predators.

Beside the deterring effect of faeces on predators Simmons (1955) expects a prominent secondary benefit of defecation in the context of predator avoidance due to reduction of start weight and thereby acceleration of starting speed of fleeing birds. Lilliendahl (2000) describes defecation for captive greenfinches (*Carduelis chloris*) exposed to a predator and supposes that this reduction in mass makes take-off easier.

In the examples above defecation has been described as part of a broader behavioural complex and with an additional meaning for the species besides depositing metabolic waste especially in respect to predator avoidance.

In this study defecation behaviour of the grey partridge (*Perdix perdix*) was examined at night time and discussed in the context of predator avoidance behaviour against the background of a night-time environment dominated by the risk of predation by the red fox (*Vulpes vulpes*).

Watson *et al.* (2007) estimate that fox predation accounts for 44% of the natural mortality of the grey partridge during winter. This is despite measures undertaken to reduce the number of foxes and the well known anti-predation measures that these partridges take to avoid predation by foxes which hunt at night using scent. For example they roost quietly in open places with good all round visibility and they fly rather than walk to their roosting sites, presumably to break the scent trail (Potts 1986; Tillmann 2006). However, little is known because the interactions between predators and partridges take place in darkness.

The defecation behaviour of grey partridges has not been documented and it has not been discussed in relation to escape behaviour. New technology is used here to explore this night-time behaviour, as part of a broader investigation of night-time be-

haviour of the grey partridge. This study highlights predator avoidance of partridges by means of thermography for the first time.

Study area

The data collection was conducted in 3 different regions of Germany at the spatial level of the hunting districts, where, in accordance with the federal hunting law, designated hunters could give permission to conduct this study. The regions were Soester Börde, North Rhine-Westfalia (two hunting districts), Bissendorf (one hunting district) and in Rothenburg-Wümme (three hunting districts), all in Lower Saxony ranging from 200 to 800 ha in size. Research sites were selected for landscape structural similarity and for their relatively high partridge densities to keep the effort for single covey observation low. Breeding pair densities in these areas range from 5 to 9 breeding pairs per 100 ha agricultural habitat [Tillmann, unpublished]. The landscape structure of the three areas is similar regarding field/forest ratio, field margin density, field crops and average field size. Relevant available field crops were winter rape (*Brassica napus*), winter wheat (*Triticum aestivum*), winter barley (*Hordeum vulgare*), winter rye (*Secale cereale*) and mustard (*Sinapis alba*); several fields were ploughed for spring sowings or were set aside; hedges, ditches and grassy tracks are also a common feature of these agricultural landscapes.

From the perspective of partridge ecology the predatory environment can be described as similar in the three research sites. At night and at twilight the most common potential predator and “disturber” is the red fox, followed by the domestic (feral and straying) cat (*Felis catus*), badger (*Meles meles*), beech marten (*Martes foina*), polecat (*Mustela putorius*), stoat (*Mustela erminea*), domestic dog (*Canis lupus familiaris*) (usually with the owner but running loose) and more locally the eagle owl (*Bubo bubo*).

Materials and Methods

In this study thermography was used to detect partridges at night and to analyse the defecation rate after the roosting partridges had been flushed. Two different infrared camera systems were used. For recording the whole complex of roosting and escape behaviour the thermal camera Raytheon “PalmIR 250 D” was used. Its wave

band range covers 7-14 μm , black and white with an array of 320 x 240 pixels. The frame rate is around 25 Hz. Noise equivalent temperature difference (NETD) as the most commonly accepted measure of infrared detector sensitivity has a value of < 0.1 °C at 30°C. It is defined as temperature differential between two adjacent elements in the scene that will give a signal to the system. The infrared camera weighs 1.75 kg and is as easy to handle as a standard handheld camcorder. To record the partridge observations for later analysis the infrared camera was connected to a Sony digital video camera recorder DCR-TRV33E. Thermal images of roosting impressions immediately after partridges had left their roosting site were taken as well as surface temperature of partridges was measured with the thermocamera ThermoCAM™ P25 of FLIR Systems. It has a thermal sensitivity of 0.08 °C at 30 °C; the spectral range covers 7.5-13 μm . The frame rate is about 60 Hz and it weighs 1.4 kg.

An average of 200 ha was scanned for partridges per night with an average effort of 5 hours per night totalling 85 scanning hours. All available habitats were considered except for closed forests. Since thermal radiation does not penetrate plants, the thermographical visibility of partridges in higher vegetation is limited. Such set-aside fields of greencover or fields of white mustard (*Sinapis alba*) were therefore entered on foot to ensure a complete survey. In crops not higher than 10 cm partridges can be seen up to a distance of 200 m with a thermocamera. Except for greencover set-aside and white mustard all wintering crops were lower than 10 cm. As survey points, topographically exposed sites or crossroads were chosen to scan an area as large as possible and to consider all available habitat types. In a few cases the camera was used from a moving car.

The observations were conducted in wintertime between 15 November 2005 and 15 February 2006, starting at around two hours after sunset to ensure that the nighttime situation was settled. Most observations were made at around 21:00 CET, the earliest at 18:40 and the latest at 00:05 CET.

As the pattern of escape behaviour of partridges from an approaching observer was expected to be somewhat affected by approaching speed (see also Cooper 1997) and directness of approach (Burger and Gochfeld 1981; Cooper 2003) these factors were standardised. Usually the partridges were detected from the road and then approached at a right angle from the road in a straight line. When a covey was detected it was approached on foot at a steady pace of ~ 0.5 m/s as silently as possible. The target covey always had a direct line of sight to the approaching observer regardless of the overall habitat visibility. Humans are regularly used as an alarming

stimulus in studies to assess anti-predator behaviour (Fernandez et al. 2004; Boyer et al. 2006), though drawbacks of using the investigator as predator are that partridges might react differently to a natural predator's approach (Cooper 2003). With the camcorder the vision of the infrared camera was recorded. The flight initiation distance FID as the distance between the predator and the prey when the partridge takes to flight was easily measured in snowy conditions and also the roosting sites could be discovered by the excrements with a flashlight. Except for the FID all the behavioural traits were analysed after digitising the records on the computer.

Approaching a covey more than once per night was easily avoided as the new roosting site of the covey was recorded and marked on a map. Similarly, approaching coveys a second time between two observation nights was avoided by choosing different sections of the study area. Between two observation nights in one study area there was a time delay of at least 7 days. However, monitoring the behaviour of a covey a second time could not be absolutely avoided given an average home range size in winter of 14 ha according to Buner et al. (2005).

The analysis considers the behavioural complex of flight behaviour until settling again with special focus on the defecation behaviour. The variables considered here are:

- 1) covey size [n individuals]
- 2) FID [m]
- 3) flight character
 - 1 direct take-off of all individuals
 - 2 direct take-off - few individuals run a few steps before take-off
 - 3 all individuals run at least 5 m before take-off
 - 4 all individuals run away – no take-off
- 4) defecation when flushed
 - 0 no defecation
 - 1 each individual defecates ca. once
 - 2 each individual defecates more than once

As environmental parameters

- 1) time [min. after sunset]
- 2) habitat characteristics
 - a) crop type [1-8]
 - b) vegetation height [cm]
 - c) soil condition [1 = soaked, 2 = moist, unfreezing, 3 = frozen]

- 3) cloud amount [%]
 - 4) snow cover [%]
 - 5) snow depth [cm]
 - 6) air temperature [°C]
 - 7) precipitation
 - 1 Shower (short downpour with large raindrops)
 - 2 Drizzle (the finest formation of droplets)
 - 3 Steady rain (long, steady rain with medium-sized drops)
 - 4 Drizzle (small drops over a longer period of time)
 - 5 Slight snow-fall
 - 6 Average snow-fall
 - 8) light intensity [1-3]
 - 9) wind force [0-8 on the basis of the Beaufort wind scale]
 - 10) moon phase [100% = full moon]
- was recorded for each located covey.

In a logistic regression of defecation behaviour with the considered variables the two defecation classes were clustered so that two classes existed: 1) no defecation, 2) defecation.

The assumptions of normality and homogeneity of variance were tested using Kolmogorov-Smirnov and Levene's tests, respectively. All statistical comparisons were two-tailed, with an alpha level of 0.05.

Results

A total of 85 scanning hours were carried out between 15 November 2005 and 15 February 2006. In this time, 640 grey partridges in 102 partridge coveys (mean number of individuals in covey 6.27, SE = 0.35) were detected, of which the flight behaviour concerning defecation could be analysed on 93 occasions.

The defecation behaviour of flushed partridges could easily be analysed on the thermographical records. Measurements of the surface temperature of roosting partridges for 6 individuals of one covey gave a temperature range of 10 °C (back plumage) to 16 °C (head). Therefore, temperature differential to the ambient temperature that ranged during the observations from -6 to +5 °C (mean = -0.13; SE = 0.27) was sufficient to depict a clear vision of roosting and fleeing partridges.

Flight initiation distance ranged from 7 to 70 m (mean FID = 22.8 m; SE = 1.13).

On 99 occasions the flight character of the individuals of the covey could be classified as shown in Fig. 1.

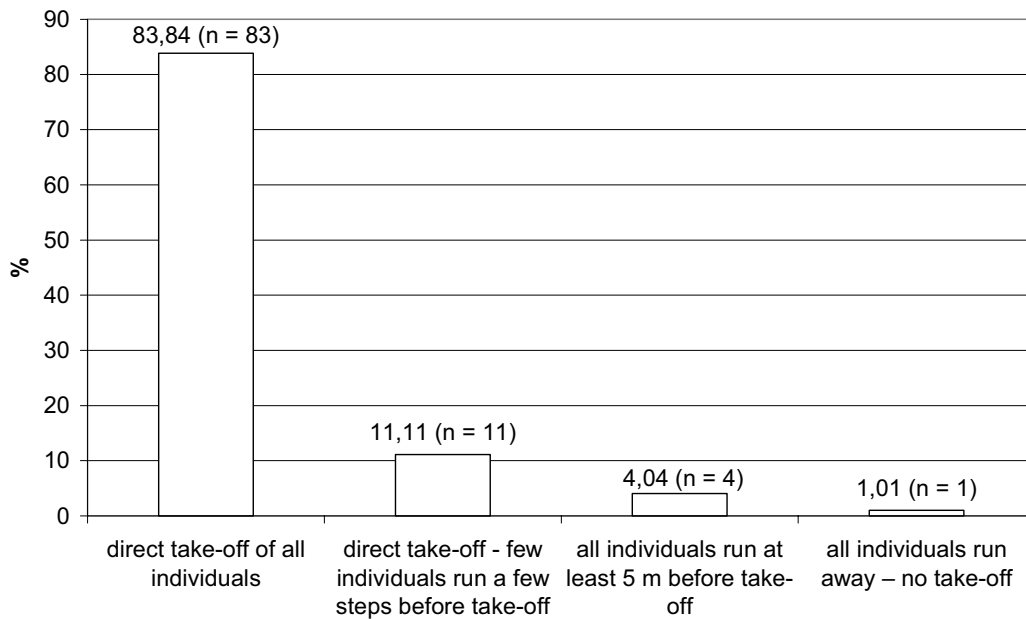


Fig. 1 Flight character of partridge coveys at night

Figure 1 shows that in almost 95% of the flushed coveys most of the grey partridges took off directly and mostly synchronously from the roosting site (Fig. 2). Of these 95% (n = 94), only in 11 coveys did a few individuals make a few steps in more or less a direct line away from the slowly approaching observer before starting the escape flight.

The straight-line of the escape flight (FD) could be estimated in 98 flushed coveys. It ranged from 50 to 250 m (mean FD = 125.71; SE = 4.86).

On 95 occasions the entire escape flight until settling again could be recorded. As freshly excreted faeces equal approximately the body core temperature of partridges of 40.5 °C the faeces appeared bright white on the display despite its small size, well distinguished from the background (Fig. 3). The droppings were excreted as separate, distinguishable units. Up to four droppings were excreted in quick succession per individual. In larger coveys defecation appeared like a “rain” of droppings. A covey of 15 partridges could for example produce up to 60 droppings more or less

evenly distributed over an area of an estimated 200 m². A starting covey in which the individuals roosted relatively close together “produces” a cluttered thermographical picture with limitations in distinguishing details (Fig. 2). Therefore, the results might be biased because of technical restriction. It is expected that due to these restrictions in analysing the thermographical records the percentage of coveys in which defecation occurs upon being flushed, 75.3%, could be greatly underestimated (compare Fig. 4).

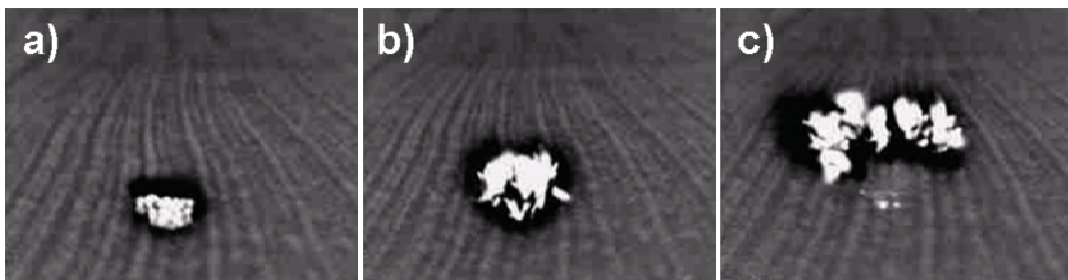


Fig. 2 Thermographical pictures of a roosting grey partridge covey (12 individuals) at night-time on winter seed a) and its initial stage of flush b), c)

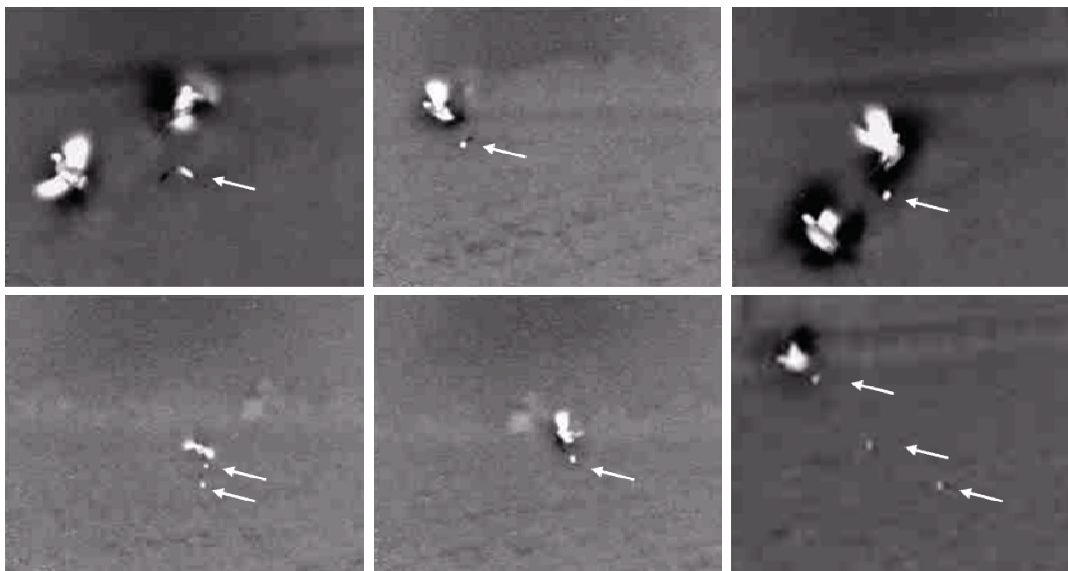


Fig. 3 Examples of thermographical pictures of flushed partridges defecating

To determine the amount of faeces excreted during escape flight and assuming the droppings excreted during the escape flight are similar units concerning weight compared to the droppings found in the roosting site fresh droppings were collected

from the roosting dents right after the partridges had been flushed. The weight of the droppings ranged between 0.38 and 1.3 g ($n = 221$, mean = 1.04 g, SE = 0.015).

Partridges usually defecated within the first 20 m of the escape flight though most droppings were excreted during the process of taking off and gaining height within the first few metres. Defecation was never observed in any individual close to the landing location. In a few instances ($n = 5$ coveys with a total of 39 individual partridges) when the FID was only approximately 10 m the roosting site could be reached early enough to be able to check individual roosting dents thermographically for freshly excreted faeces. In 4 instances (10.26 %) freshly excreted droplets were found in roosting dents of individual partridges. These droplets must have been excreted right before take-off or right after take-off. Using the FLIR-System [methods] freshly excreted faeces could be easily detected if the roosting site was reached within approximately 5 s after the partridge had left its roosting position and cooling down of the faeces had not progressed too far.

In 93 escape flights of various coveys (individual partridges = 569) the thermographical records could be analysed for defecation behaviour. No partridge defecated in 24.7 % of the flushed coveys; in 62.4 % of the flushed coveys each individual defecated approximately once during the escape flight; "excessive" defecation with more than one and up to four excreted droppings per individual was detected in 12.9 % of the flushed coveys (Fig. 4).

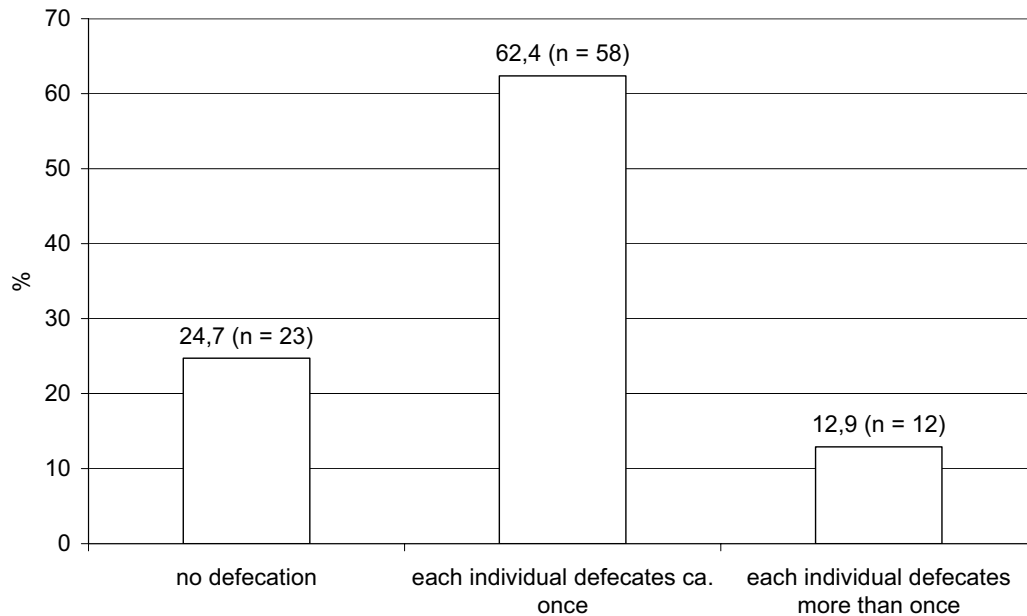


Fig. 4 Defecation behaviour in 93 flushed partridge coveys

Flight initiation distance did not significantly differ between the three classes as regards defecation behaviour (Kruskall Wallis Test, $df = 2$, $p = 0.106$) despite FID tending to be lower in the class “each individual defecates more than once” ($n = 12$, mean = 18.17, SE = 2.777) than in the class “each individual defecates circa once” ($n = 58$, mean = 24.10, SE = 1.623) and in the class “no defecation” ($n = 23$, mean = 24.83, SE = 2.020).

For none of the considered variables, i.e.

1) time [min. after sunset], 2) moon phase, 3) cloud amount, 4) snow cover, 5) snow depth, 6) temperature, 7) covey size, 8) FID, 9) FD, 10) vegetation height, 11) vegetation cover, could a relation to defecation behaviour be identified.

Defecation behaviour was not correlated with soil condition at the roosting site (Pearson’s chi square, $df = 2$, $p = 0.914$), crop type (Pearson’s chi square, $df = 7$, $p = 0.394$), light intensity (Pearson’s chi square, $df = 2$, $p = 0.166$), precipitation character (Pearson’s chi square, $df = 4$, $p = 0.556$), and not with wind force (Pearson’s chi square, $df = 3$, $p = 0.128$).

During the 85 observation and scanning hours numerous potential predators for the partridge were detected, most often the red fox and straying cats. In a few cases beech martens (*Martes foina*) and badgers (*Meles meles*) were observed. Stoats

were never observed using a thermocamera despite their common occurrence. Most often predators had detected the observer and only their fleeing behaviour could be recorded. Comparing roosting sites with the location where the predators were detected, foxes are the main threat to partridges at night in a winter situation as they also run across fields searching predominantly by scent for food and do not show a strict bond to margin biotopes in their spatial behaviour. The other predators usually searched for food along field margins and hedges where partridges do not roost.

Discussion

A potential advantage of defecation of birds in a threatening situation or when being directly attacked by a predator is that defecation may lighten birds and thus increase their chances of escape. In principle this positive selection of defecation before flying is independent of a direct threat as all behavioural components should be selected for energy efficiency. In this study grey partridges were observed excreting four droppings at most per individual per escape flight. Underlying the determined 1.04 g per dropping 4.16 g faeces are excreted per escape flight at maximum. This amounts to approximately 1.1 % of the average bodyweight of 380 g of a partridge as reviewed by Dwenger (1991). For the grey partridge the positive selective effect is therefore expected to be rather marginal but evolutionarily not impossible as reduction in weight not only indicates accelerated flight and therefore higher escape probability but also reduces flying costs in terms of energetic expenditure independent of a threat.

Defecation in birds as in other vertebrates in a threatening situation belongs primarily to the flight instinct and in its evolutionary origin does not belong to the context of aggressive defence or protective strategies. Nonetheless, defecation as vegetative epiphenomenon of fear evolutionarily has become secondarily useful in some bird species as the examples in the introduction show.

The common occurrence of defecation in the grey partridge during the initial stage of escape flight and not before taking off as to be observed in other bird species leads to the attempt to also discuss this behaviour in the context of predator avoidance. The most relevant ground dwelling predator of the partridge at night time is the red fox (Reynolds and Tapper 1995). If the fox in the process of attacking a flushed partridge is hit by faeces an instantaneous deterring effect can be expected. Additionally, defecation might strengthen the direct confusion effect in a simultaneously

starting partridge covey. As fleeing may prevent fitness-enhancing/beneficial activities (Cooper and Frederick 2007) the decision to start escaping is postponed as long as possible to assess whether an approaching predator really has detected it. Theoretically partridges can trust longer in remaining motionless and maintaining crypsis longer since defecation when attacked has a high potential to deter an attacking predator as evidenced for other bird species.

In addition to the direct deterring effect of defecation for predators it is hypothesised here that defecation in fleeing partridges has an indirect beneficial value for avoiding predation by confusing predators. The analysis of the thermographical records of the escape flight revealed that in most coveys individuals defecate during the initial stage of flush and up to 20 m at maximum away from the roosting position. The excretion of faeces in a covey appeared like a “rain” of droppings. As mammalian nocturnal predators strongly rely on their sense of smell it is supposed that this faeces creates an odorous cloud that olfactory blinds spatially and temporarily. In a similar context Mester (1976) discusses the effect of defecation in the little grebe (*Podiceps ruficollis*). The author assumes that the faecal cloud left behind in the water right after diving away from an attacking predator might camouflage the escape route, the faeces having an optically confusing effect in the same way as the ink of an octopus may confuse a predator. Additionally, the irregular spreading of droppings observed in a flushed grey partridge has the potential to preoccupy and confuse predators searching for tracks of further partridges to a certain extent. Given the great distance at which predators such as the fox can detect their prey by scent it is likely that this odorous cloud-effect obliterates a sharp picture of the direction in which the covey fled. Thus, the chance of a subsequent second attack of the same predator on the covey at its new roosting location is somewhat reduced. The odorous fog evolutionary also might have supported selection for a shorter flight distance saving energy. With a shorter flight distance the covey potentially does not have to leave the area that has been chosen for spending the night in and therefore the risk of fleeing to an unknown environment is reduced and the survival probability increased.

In many cases partridge coveys instead of walking, fly to their well chosen roosting place at dusk. This behaviour can be interpreted as predator avoidance as the place is left where the partridges spent the evening foraging, dusting etc., leaving many odour tracks on the ground that would lead olfactory oriented predators directly to them. Flying is an additional energetic expenditure for a predominantly ground

dwelling bird. This is particularly relevant in view of the fact that the partridge flies voluntarily less than a minute per day when not forced to fly away (Blank and Ash 1956). Under the permanent predatory pressure partridge behaviour has been selected for minimisation of the production of odorous tracks. This assumption is supported by Homberger (pers. comm. 2007) who finds that breeding partridges leaving the nest for recreation and comfort behaviour do not defecate before being 133 m ($n = 11$, $SE = 6.99$) away from the clutch. This provides further evidence that in this situation droplets are instinctively treated as potential attractants to predators in partridge behaviour, thus supporting the theory that droplets excreted during the initial stage of flush may have a sidetracking, occupying effect on predators. Defecation right after being flushed also delays defecation and therefore production of additional odour tracks at the new roosting site, thereby reducing the chance of olfactory detection at the new roosting site.

It is assumed that in most cases partridges detected the approaching observer both acoustically and visually before responding to this stimulus with a change in behaviour, i.e. fleeing. This assumption is supported by the fact that in most cases all individuals of a partridge covey started their escape flight simultaneously. Further, in many cases it could be noticed from the thermographical records that single partridges started to move and crane their head prior to fleeing as opposed to motionless roosting when observing the partridges from a far distance. It appeared that the grey partridge took time in making a discreet decision after detecting the approaching observer as predator stimulus to then fly away as the observer slowly approached. Considering the mean FID of 22.8 m defecation occurred on most occasions without a direct life-threatening situation. Apparently fright defecation, as original parasympathetic reaction as described for various bird species by Mester (1976), has become chronologically uncoupled in the course of evolution from an imminently life-threatening predator attack in the grey partridge.

The use of metabolic products is common in anti-predatory defence strategies of animals deterring a predator (Caro 2005). Specialised defensive secretion by special glands found in all animal classes proves to be an evolutionary success. Various vertebrates produce toxic, caustic or disgusting secretions in specialised glands as a chemical defence strategy. Defensive secretion is always combined with energetic expenditure. But, also defensive defecation in birds can presumably be combined with energetic expenditure if faecal material that was still being processed in the gut was ejected prematurely from an energetic perspective. In addition to the loss of

energy a dehydration effect is possible. By contrast, defensive defecation in the grey partridge requires no energetic costs as only “mature” faecal material was ejected. Therefore, defecating energetically should be absolutely efficient as part of anti-predator behaviour. All anti-predator adaptations are multi-step processes and every step should be selected for its efficiency (Lima and Dill 1990; Boyer et al. 2006). The functional integration of defecation in the complex of predator avoidance behaviour of the grey partridge but also in other birds satisfies this theorem.

This study provides evidence that defecation as an originally parasympathetic reaction towards threat during the initial stage of escape flight in partridges has functionally been secondarily integrated into escape behaviour and selectively been shaped towards effectiveness concerning predator avoidance. Defecation in the behavioural complex of predator avoidance hypothetically has various beneficial selective effects. Further, it is free of any additional energy costs in contrast to many other steps in predator avoidance strategies. This is the first time defecation behaviour in fleeing partridges has been described and discussed in connection with predator avoidance.

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Kapitel V

**Evaluation of hunters' spring pair density estimations of the grey partridge
(*Perdix perdix* L.)**

Tillmann J.E. (2009)

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Introduction

According to historic literature the grey partridge (*Perdix perdix*) population in Western Europe probably had its highest density in the 18th century (Tillmann 2006). However, until the late 1970s the partridge was still one of the most common birds in agricultural landscapes in Germany and of extraordinary significance as a game bird. Until 1978 partridge populations always recovered from high mortality rates and population collapses during severe winters as happened for example after the exceptionally hard winter of 1962/63. The r-strategic partridge with one of the highest reproduction potentials in birds - given its average clutch size of 15 eggs (for review see Dwenger 1991) – could easily compensate for population losses due to severe winters, predation or high hunting pressure. It was the winter of 1978/79, characterised by a prolonged snow cover in combination with exceptionally unfavourable weather conditions during the reproduction seasons from 1979-1981 which resulted in a nationwide population collapse from which the grey partridge has never recovered. In suboptimal partridge habitats, such as submontaneous landscapes with a high proportion of forest cover, it was even exterminated and in arable landscapes its typical habitat population densities of the highly vulnerable flagship species diminished to a minimum. Average spring densities in its currently populated habitats in Germany are around one pair per 100 ha (compare Pegel 1987, Tillmann et al. 2007). This population history is representative of a dramatic decline in partridge numbers throughout its European range (compare Potts and Aebischer 1995, Hagemeyer and Blair 1997, Bro et al. 2001; Aebischer and Ewald 2004; De Leo et al. 2004; Panek 2005). The reasons for partridge populations remaining at such a low level are manifold and discussed elsewhere (e.g. Tucker and Heath 1994, Potts 1997, Hagemeyer and Blair 1997, Putaala and Hissa 1998, Bro et al. 2000, Joannon et al. 2008).

In Lower Saxony, the second largest state in Germany, data on grey partridge hunting bags have been continuously collected since 1957. In the year 1959 167,712 partridges were bagged compared with only 3,254 in 2006, corresponding to a dramatic decline of 98.1 %, indicating a cutback almost to insignificance as a game bird (compare Fig. 1).

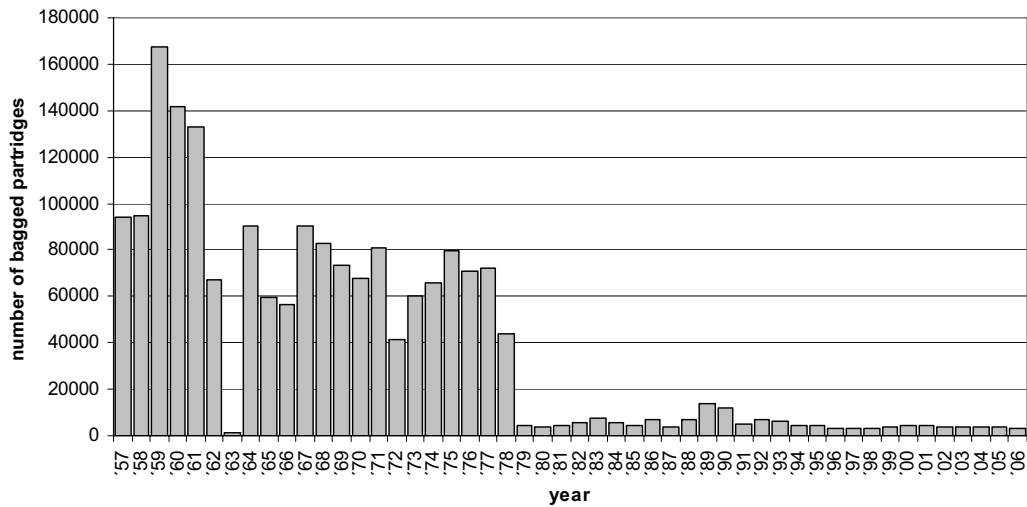


Fig. 1 Number of partridges bagged in Lower Saxony, Germany between 1957 and 2006 (Tillmann et al. 2007)

The “unfavourable conservation status” of the grey partridge across the continent, as a result of substantial declines (Tucker and Heath 1994), gave in the same breath rise to the question of the huntability of the grey partridge. According to the Red List of breeding birds the grey partridge is of conservation concern in every federal German state, being categorised between 1 (critically endangered) and 3 (vulnerable). In Lower Saxony up to 2006 the grey partridge was listed as critically endangered on the Red List (Südbeck and Wendt 2002). In the new edition of the Red List of threatened birds in Lower Saxony (Krüger and Oltmanns 2007) the grey partridge is only listed as endangered owing not to a significant population recovery but rather to a much more comprehensive survey of its status compared to the data basis of the list from 2002 (Tillmann et al. 2007).

On the other hand the grey partridge still has an open hunting season in 13 out of the 16 federal states in Germany; in two of those 13 federal states the responsible Ministries and hunting associations asked hunters to voluntarily refrain from hunting partridges and in another three states hunting partridges is voluntarily restricted depending on spring pair densities and/or autumn densities. A conflict has generated between the conservation status of the grey partridge on the one hand and the fact that it still being hunted on the other hand.

It is well accepted that decisions concerning the management and conservation of wildlife have to be based on discreet information on the population status and dy-

namics and the distribution of the respective wildlife species. Consequently hunting associations have been increasingly concerned with gathering data on wildlife populations to document the sustainability of hunting, to evaluate spatio-temporal changes in wildlife populations and changes in wildlife utilisation.

With the aim of monitoring wildlife populations, assessing hunting modalities and of providing a database for decisions in the context of the hunting law and guidelines, the Hunting Association of Lower Saxony (Landesjägerschaft Niedersachsen, LNJ) introduced the monitoring program “Game Survey Lower Saxony” (“Wildtiererfassung in Niedersachsen”, WTE) in 1991 (Pohlmeyer & Strauss 2006, Strauss 2008). State-wide, every year owners or tenants of each of the 8,911 hunting districts are asked per mail to respond to a questionnaire about their estimation of the numbers of partridge pairs in spring and among other questions about other wildlife species or for example land use modalities in their hunting district. Participation in this postal survey is traditionally relatively high with 80-90 % each year (compare White et al. 2005). In 2005 88.9 % (n = 7918 private hunting districts) returned the completed questionnaire, representing approximately 85 % (= 34900 km²) of the huntable area of Lower Saxony (compare Pohlmeyer & Strauss 2006, Tillmann et al. 2007, Strauss 2008). However, these data provided by hunters are subject to much criticism. The objections include the validity of the data gathered by hunters as little is known how hunters arrive at their estimations and as to whether their data might be politically motivated. In this study for the first time hunters` estimations on partridge densities are evaluated using the example of the WTE in Lower Saxony. Data accuracy is assessed by ground truthing and the data quality discussed in light of the background of the social environment of the responsible hunters.

Methods

Lower Saxony is with almost 48000 km² the second largest federal state of Germany. Lower Saxony borders on (from the north and clockwise) the North Sea, the states of Schleswig-Holstein, Hamburg, Mecklenburg-Western Pomerania, Brandenburg, Saxony-Anhalt, Thuringia, Hesse and North Rhine-Westphalia, and the Netherlands. The altitude ranges from 2.05 m b. s. l. and 971 m a. s. l. The northern half of Lower Saxony, the North German Plains, is almost consistently flat except for the gentle hills around the Bremen Geestland. The northern parts of the German Central Highlands, the Weser mountain range and the Harz Mountains lie towards the south

and southwest. Between these lies the Lower Saxon Hill Country, a range of minor elevations. 61 % of the states` area is used agriculturally and 21 % is covered by forests. Of the 61 % agricultural land 25 % is permanent grassland; as for the main crops, acreage corn covers 49.6 %, root crops (sugar beet, potatoes) 5.4 %, maize 4.7 %, legumes 0.4 % and 6.8 % of the arable land is set aside (according to LSKN 2005). The annual precipitation ranges between 550 and 900 mm / a in the regions characterised by farming as the most relevant partridge habitats. The annual average temperature is 8 °C and the climate is Atlantic to sub-Atlantic in the west and north west with an increasing continental character towards the east and south east. In order to evaluate the WTE a total of 123 hunting districts in Lower Saxony were randomly chosen. The hunting districts had to fulfil the following criteria: the tenants or owners of the hunting district had to have participated in the WTE on a regular basis and the hunting districts had to be at least 200 ha in size. To only select hunting districts with a minimum of 100 ha potential partridge habitat only those were accepted with a maximum share in forest cover of 50 %. The evaluation took place during the springs of 2002-2006. As seen in table 1 the evaluation of the WTE was conducted in a total of 123 hunting districts.

Tab. 1 Number of hunting districts per year in which ground-truth survey were conducted

Year	2002	2003	2004	2005	2006	Total
Number of hunting districts	37	36	19	15	16	123

To evaluate the hunters` estimations area-wide the spring call counts were conducted to exactly the same extent as in the hunting district but focussing only on the potential open partridge habitat, therefore excluding closed forests and larger settlements. Common methods for determining spring densities of the grey partridge are based on varying approaches to counting calling cocks (e.g. Illner 1992, Panek 1998, Panek 2006).

The characteristic “rusty gate call” of grey partridge cocks starts to occur more frequently after covey break-up in February, but most commonly between mid-March and the end of April - during the pairing and pair season before the nesting season when partridges live again very cryptically and rather silently. Additionally, during this

period the chance to see partridge pairs at dawn is relatively high because of their extroverted display behaviour. Consequently, this period with the highest vocal activity from 15 min. after sunset continuing for 30 to 45 min until total darkness (see Rotella & Ratti 1986, 1988, Panek 1998, Voigt 1999) was chosen to determine spring pair densities. At this stage, approximately from 4 weeks before the first egg is laid onwards, partridges are already relatively site confident so that the detected partridges are representative for the considered site.

The method used here is a combination of the standardised but relatively time- and labour-intensive method introduced by Pegel (1986) with the "point-stop-count" as described by Bibby et al. (2000).

On a topographical map (1:25000) of each hunting district the line transects with a length of between 1000 and 1500 m, this having been established in a geographical information system (GIS - ARCVIEW 3.2) predominately oriented to the existing road network, field borders or other accessible linear landscape features. The transects were at least 300 m but no more than 500 m apart from each other. To check for a complete "acoustical coverage" the transects were buffered by a 200 m hem in the GIS. The number of transects needed to cover the study site was on a par with the number of observers needed. The distance between the survey transects is a result of the acoustical reach of the rusty gate call that can usually be heard up to a distance of 100 to 300 m depending on the environmental noise and landscape structure as own tests revealed. The acoustical coverage of one line-transect and one person respectively therefore ranges between 56 and 76 ha with this method. The length of the line transects results from the peak call activity phase of partridges that begins 15 min. after sunset and lasts 30 - 45 min. (see Panek 1998); with four breaks of 5 min. each and a slow steady walking pace 1000-1500 m could be comfortably covered during the targeted 40-60 min. duration of the count. The four stops were placed if possible, these being obvious from the topographic map, at topographically exposed positions and at more or less even distances apart (i.e. 333-500 m), starting with the first stop at the beginning of the transect with the last point at the end of the transect. These 5 min. stops were established to give the observers the chance to intensively concentrate and interpret the acoustical environment without being distracted by their own footsteps and breathing, therefore improving the probability of detecting calling cocks at greater distances.

During January of each year the tenants or owners of the randomly chosen hunting districts were contacted via telephone. They were given a brief introduction to the

partridge monitoring program and the time effort involved. However, no mention was made of the main intention of the study, namely to evaluate the WTE so as not to motivate them to count the partridges in advance of the official count to improve their estimation. Tenants or owners of randomly chosen hunting districts who insisted that no grey partridges lived on their hunting district were persuaded that this in-depth monitoring was necessary in order to gain an overall impression of grey partridge densities in Lower Saxony. The majority of the volunteers in the counts had to be provided by the contacted tenants. With the survey method described below between 16 and 18 people were needed per 1000 ha. The counts were organised and coordinated by a field researcher from the Institute of Wildlife Research and a field ornithologist from the Ornithological Station of Lower Saxony (Staatliche Vogelschutzstelle Niedersachsen) to guarantee that the standardised method was adhered to and that consistency was maximised. Additionally a questionnaire survey on the quality of the method was conducted among the 123 assisting field ornithologists. The ornithologists were asked to qualify this total census method from a specialist's view respecting the applicability of the method and the reliability of the yielded partridge pair densities.

All surveys during the 5-year study were appointed between 15 March - 30 April and in consultation with the contact person of each hunting district the date for the survey was set two weeks in advance. The contact person was told how many participants were needed. The exact time of sunset was determined in advance, corresponding to the geographical coordinates of the respective hunting districts and as a meeting point usually the home of the owner or tenant of the hunting district was agreed upon. The point in time when the participants of the survey met was on average $\frac{3}{4}$ of an hour before the survey had to begin. The time was used to give a short introduction on partridge ecology and to brief all observers on the survey method. To envision the vocalisations of grey partridges the whole set of calls to be heard potentially were played on a tape recorder. By way of a general map of the hunting district the participants were shown the local environment, if not already familiar with it, and every participant was assigned one of the numbered line transects as marked on the map. Every observer was handed out a hard-backed notebook, a pen and a detailed map section with the respective line transect in A 4 size with a scale bar. Additionally, a small form was printed on the map on which each observer was asked to fill in all observations made. In one of the two columns the type of observation had to be noted, i.e. rusty gate call, the number of calls or partridges being observed and in the

other column the respective times to the minute of the observations were noted. Corresponding to the consecutive numbering of the observations the observations were marked exactly on the map in the case of optical observations and in the case of an “acoustical observation” with the assumed location of the partridge. If partridges were flushed the direction of the escape flight was sketched in and if possible also the landing position. After the survey each participant was asked about his observations which were then marked on a general map with the respective time of the observation, thus excluding double counts on this basis as a potential source of bias. The transport of the observers was organised in such a way that all observers were able to begin with the counting at exactly the same time. The survey was conducted in all of the 123 hunting districts a second time after at least 4 days and not later than 10 days, following the same procedure except that the observers started from the other end of the line-transects. The survey was repeated a third time if the variation coefficient between the two counts was greater than 25 %.

The acoustical and optical partridge observation of the two counts per hunting district were categorised as follows: “probable breeding” (PrB) – a locally established breeding pair - was assumed once a partridge pair had been observed at one of the two counts. When a pair was also observed at the other count within a radius of 150 m around the first count this pair was assumed to be the same. When at one count a partridge had been heard or seen but within the radius of 150 m around that observation no evidence of it was found at the second count it was categorised as “possible breeding” (PoB); in case a partridge could be acoustically or optically detected at both surveys within a perimeter of 300 m it was categorised also as probable breeding (PrB). Due to this single piece of evidence of a partridge being at a certain location and given the male surplus in partridge populations as described e.g. by Szederjei et al. (1959) or Dwenger (1991) PoBs counted only for 0.5 breeding pairs (BPC), whereas PrBs were considered as directly representing a breeding pair. The radius of 150 m was chosen as the respective circle covers an area of 7.1 ha which reflects the lower end of the territory size in the grey partridge before nesting and before the breeding season (compare Döring and Helfrich 1986; Panek 2002; Šálek et al. 2002).

Assumptions underlying the statistical tests used in this study, normality and homogeneity of variance were checked using Kolmogorov-Smirnoff and Levene’s tests, respectively. When the assumption of normality was satisfied the distribution of the

variables was characterised by the arithmetic mean (mean) and the standard error of the arithmetic mean (SE). Otherwise, it was characterised by the median and the 25th and the 75th percentile (p25 and p75) respectively. To compare the data resulting from counts and estimations Wilcoxon signed rank test was applied. To test for correlation the test Spearman Rank Correlation was applied as the considered data were not normally distributed.

All statistical comparisons were two-tailed, with an alpha level of 0.05. The statistical analyses were performed using SAS statistical package version 9.1 (SAS Institute Inc., Cary, NC, USA) and SPSS version 16.0 (SPSS Inc., Chicago, IL, USA).

Results

More than 90 % of the initially contacted tenants or owners of hunting districts agreed to participate in the grey partridge count. The other almost 10 % declined due to disinterest, lack of time or lack of potential participants in the count. On average 9 people participated in the counts given the average size of the hunting districts of 652.5 ha with a share of open landscape as partridge habitat ranging between 108 and 1537 ha (arithmetic mean = 515.2; SE = 26.95). Altogether 63,846.77 ha were covered by the total census in order to ground-truth hunters estimation (BPE). With 123 hunting districts and 255 counting dates a total of 1978 people participated in the counts over the 5 study years.

The method could easily be explained to the participating observers so that they could follow the instructions unproblematically.

The questionnaire survey on the quality of the method showed that almost all of the 123 assisting field ornithologists (98%) who returned the questionnaire judged it as well qualified from a specialist view and therefore suitable as a ground-truthing method for evaluating the hunters' estimations (see Tab. 2). Moreover, using this method produced realistic (64 %) and tolerably realistic (35 %) information in spring pair densities of the grey partridge according to the opinion of the assisting field ornithologists (see also Tillmann et al. 2007).

Tab. 2: Results of the opinion poll concerning the applicability of the used spring census method and the quality of the results

a) evaluation of the method from the specialist's view				
	well qualified	to lesser extent qualified	not qualified	not specified
	120 (98 %)	2 (2 %)	0	1
b) quality of the results from the specialist's view				
	realistic	tolerably realistic	unrealistic	not specified
	79 (64 %)	43 (35 %)	1 (1 %)	0

Over the 5-year cumulative study over the 123 hunting districts 761 assured partridge detections - both acoustically or optically - were made at the first census date and 769 assured detections at the second census date. Overall 767 of those partridge observations were categorised as PrB and another 631 as PoB, resulting in 1096.5 breeding pairs (BPC) that were used for evaluating the hunters' breeding pair estimations (BPE).

In figure 2 the value distribution of the ornithological categories PrB and PoB related to 100 ha potential partridge habitat are depicted just as the resulting BPC as test statistic for the BPE of the hunters. It is to be seen that on average the partridge observations – when analysing the two survey dates - can be significantly more often classified as PrB (median = 0.95) than as PoB (median = 0.80, N = 123, Wilcoxon: p = 0.029). Comparing the resulting breeding pair density as a result of the indepth surveys (BPC) with the hunters' estimations concerning spring pair density (BPE) on average the results of the ground truthing surveys were significantly higher (median = 1.33) than the hunters' estimations (median = 1.14, N = 123, Wilcoxon: p = 0.0001).

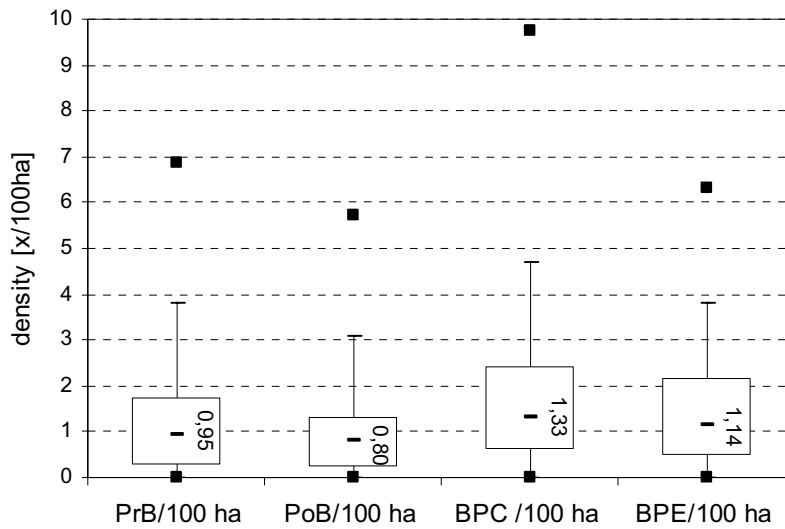


Fig. 2 PrB, PoB, BPC and BPE respectively per 100 ha [median indicated as figures within the box; boxes indicating P₂₅ and P₇₅, whiskers indicating standard deviation, squares indicating minima and maxima]

Hence, hunters underestimated the density of partridge pairs per 100 ha potential habitat on average by 0.16 (P₂₅ = -0.67, P₇₅ = 0.07) (compare Fig. 3). In 56.91 % (N = 70) of the hunting districts the partridge densities were underestimated, in 21.95 % (N = 27) the density was overestimated and in 21.13 % (N = 26) it was estimated identically compared to the total census densities. The average deviation comprising the whole data set (N = 123) and disregarding the direction of the deviation was 24.24 % (P₂₅ = 5.26, P₇₅ = 47.06).

In absolute figures hunters estimated the number of partridges pairs in their hunting district at 4.75 (P₂₅ = 2, P₇₅ = 9), whereas the ground truthing surveys resulted on average in 6.5 breeding pairs per hunting district (P₂₅ = 2, P₇₅ = 11.5). The respective underestimation by hunters counted on average for 1 pair (P₂₅ = -3, P₇₅ = 0.5) (see Fig. 4).

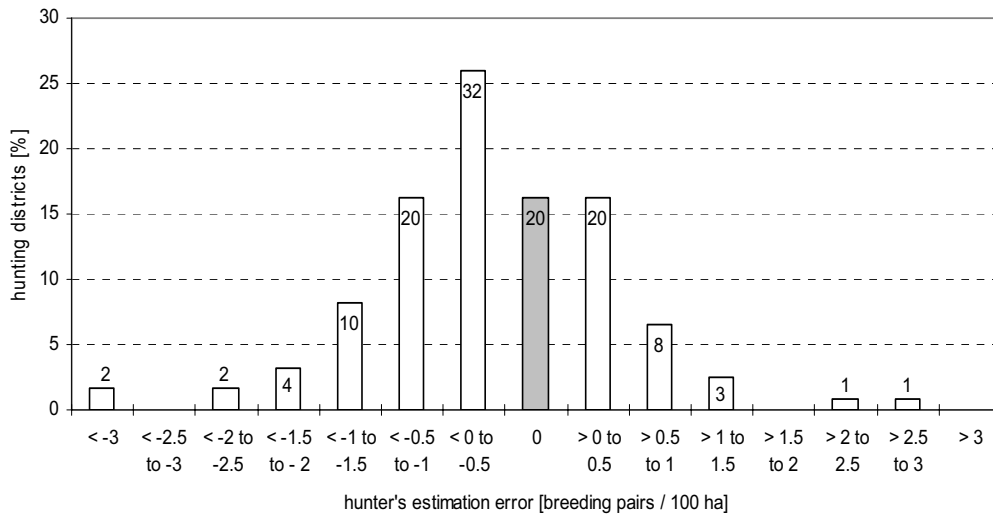


Fig. 3 Distribution of hunter's estimation quality concerning the partridge pair density per 100 ha in their hunting district compared to the ground truthing survey (N = 123; the absolute number of hunting districts is indicated in each column)

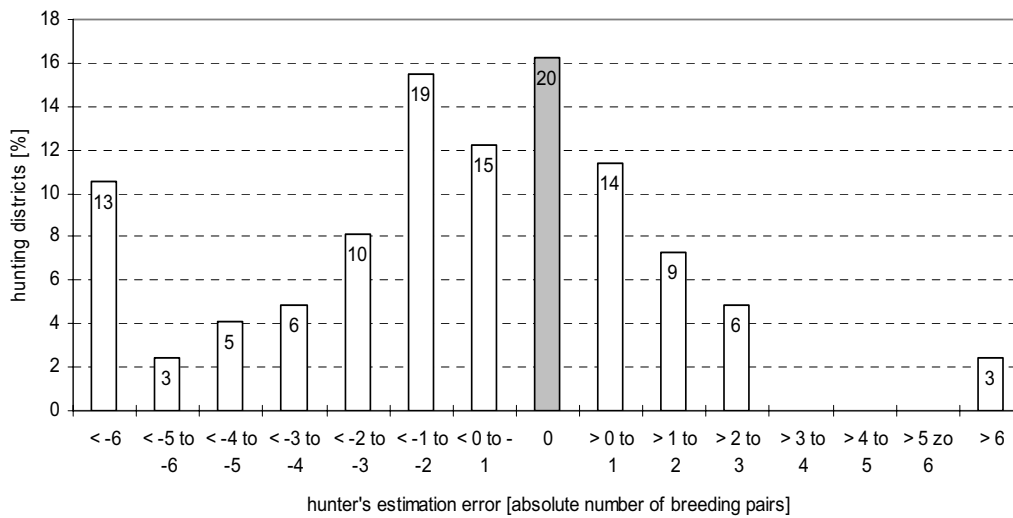


Fig. 4 Distribution of hunter's estimation quality concerning the absolute number of partridge pairs in their hunting district (N = 123; the absolute number of hunting districts is indicated in each column) compared to the ground truthing survey

The estimated breeding pair density was highly significantly positively correlated with the breeding pair density as yielded from the ground truthing surveys (Spearman Correlation Coefficient $r = 0.854$, $p < 0.0001$). In figure 5 the relation of the BPC/100 ha with the respective BPE/100 ha is depicted as scatter plot as well as the algorithm

of the corresponding generalised linear regression model. Assuming that the ground truthing census yielded unbiased results the line $x = y$ indicated as dashed line describes the ideal correlation; dots below the ideal represent underestimates.

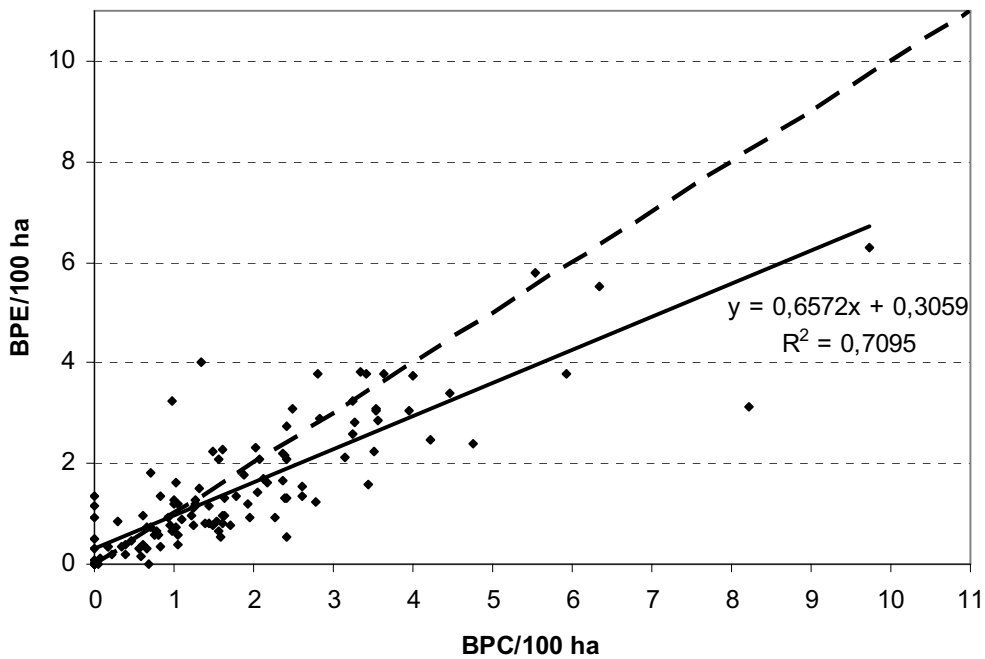


Fig. 5 Relation of BPE/100 ha and BPC/100 ha (N = 123)

The hunter's estimation error as difference of BPE/100 ha and BPC/100ha was highly significantly negatively correlated with the number of breeding pairs per 100 ha as determined in the ground truthing counts (Spearman Correlation Coefficient $r = -0.512$, $p < 0.0001$). The generalised linear model as indicated in figure 6 describes the growing estimation error the higher the partridge density is.

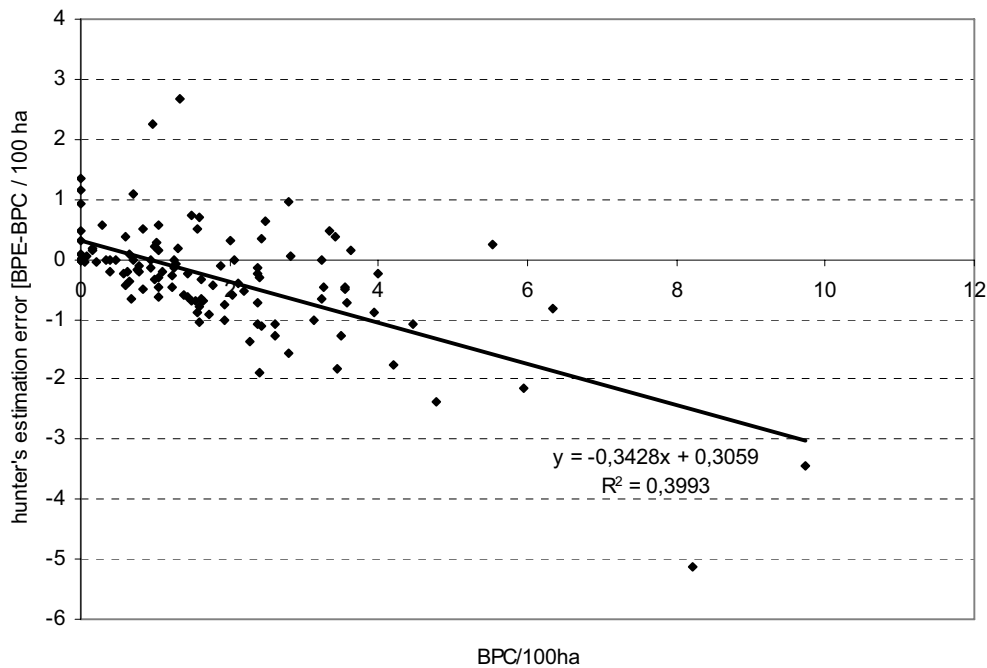


Fig. 6 Relation of hunter's estimation error and BPC/100 ha (N = 123)

After a decadic logarithmic transformation the hunter's estimation error as difference of BPE/100 ha and BPC/100 ha was negatively correlated with the size of the hunting district (Spearman Correlation Coefficient $r = -0.187$, $p = 0.0358$) meaning that the larger the hunting district is the higher the chance is of the breeding pair density being underestimated by the hunter.

Discussion

It is difficult and expensive to acquire precise and detailed population density estimates and information on the distribution of a species. Ideally, adaptive management would include continuous population monitoring over longer periods using selected indicator species (Kremen et al. 1994). The grey partridge is known to be a representative and sensitive indicator species for biodiversity in agricultural landscapes and therefore for the evaluation of the sustainability of the considered land-use system (e.g. Tillmann 2006).

Knowing the absolute densities of grey partridge pairs as reproductive stock is a fundamental indication in the study of its population status and dynamics (Pepin and

Birkan 1981). To yield large scale data on population status Middleton (1935) was the first to use beatings to determine partridge pair densities. However, this method needs too many people and too much time for it to be used in the long-term and on a large scale. Therefore, gathering data via questionnaire surveys among local hunters has the potential to yield data on the population status continuously and over a large scale for comparatively low costs. As hunters are usually not professional ornithologists the quality of their estimations has to be evaluated by ground-truthing. It is an unconditional necessity to critically assess how data generated by amateurs or data gathered via questionnaire surveys most often representing amateur estimations correspond to reality. However, according to White et al. (2005) in less than 10 % of animal surveys using questionnaires an independent verification of the facts is carried out.

Comparing different survey methods for wintering birds on farmland Atkinson et al. (2006) suggest that in order to acquire accurate data on numbers of the partridge as key species the intensive whole-area search methodology has to be applied; otherwise numbers are regularly underestimated. Whole area territory-mapping as an intensive approach is known to yield data of adequate consistency and accuracy (compare Rosenstock et al 2002, Watson 2004). The method applied in this study as labour intensive whole area search for the purpose to ground truth hunters' estimations is therefore a suitable method as the questionnaire survey among 123 field ornithologists additionally accredited. Furthermore, the repeat count in every hunting district allows for a qualification of the observation into the categories "probable breeding" and "possible breeding". The high consistency of partridges detected per transect between the two counts approves the established site confidence right before the breeding season as also found by other authors (e.g. Döring & Helfrich 1986, Potts 1986).

However, even though the method used was supposed to produce results close to the real partridge densities and therefore ideal for ground-truthing estimations it can not be ruled out that the results of the survey are no exact reflection of the real partridge densities (compare Thompson & La Sorte 2008). Biases can occur, for example when a calling cock in twilight moved its location during the survey and the change in location went unnoticed. Further sources of bias are assumed to originate from observers' sensual abilities, noise, detectability subject to habitat type or partridge activity.

The determined breeding pair densities of on average 1.3 pairs / 100 ha open landscape as found in the detailed ground-truthing surveys fit well to the average density in Germany that is around 1 pair / 100 ha in spring. The fact that some of the contacted tenants or owners of hunting districts refused to participate in the counts because of the insignificance of the partridge as a game bird on their hunting district sites with higher partridge densities might to a certain extent be overrepresented.

Comparing these total census densities with the respective estimations of the hunters, on average hunters were found to underestimate partridge spring pair densities in their hunting district. Underestimation of wildlife population densities by amateurs is a common phenomenon (see Genet & Sargent 2003, Newmann et al. 2003). The average variation of 24 % of the hunters' estimations - disregarding its direction - from the total census densities presents a remarkable accordance comparing it with other studies evaluating bird census methods (e.g. Raman 2003). The growing discrepancy of total census densities and hunters' estimations with increasing partridge densities might be due to the clarity of the situation with lower densities and *visa versa*: are the partridge densities low, the few, often the only covey is individually known and its fate can be followed over the winter. This applies accordingly to the resulting breeding pairs after covey break-up. Is the partridge density higher the picture of the number becomes more diffuse; single coveys/pairs might be mistaken with other coveys/pairs, leading to an underestimation. Concerning the increasing discrepancy between hunters' estimations and total census densities with increasing size of the hunting district it can be hypothesised that the presence phase of hunters per ha decreases with increasing size of the hunting district resulting in a rather incomplete picture of the partridge population compared to a manageable smaller area.

Even though not systematically assessed it is assumed that at least 90 % of the local hunters whose estimations were evaluated were either farmers or involved in agricultural activities. Therefore, it can be stated that in the case of small game hunting districts in agricultural landscapes in most cases local people, often the local farmers own or rent hunting districts. In few cases are the owners or tenants of hunting districts at least in touch with local farmers that lease the right to hunt their land if they do not use it themselves. Reading et al. (1996) state in respect to their questionnaire survey on the status and distribution of adders (*Vipera berus*) that farmers, compared with other respondents represent a more stable community and are therefore more likely to have been familiar with their surroundings for a longer period of time

and therefore are more likely to notice changes to their environment. The social system in rural areas traditionally supports information exchange between inhabitants of such areas and also between generations. Before the counts it could be well observed how the local volunteers from the circle of hunters and farmers discussed their recent experiences or sightings of partridges and knew very well where partridge coveys had survived the winter in their hunting district. The comprehensive year-round coverage of their local environment not only through their farming but also through their leisure activities and their interest in nature provides the local community involved in hunting a comprehensive overview of partridge presence and even population dynamics despite the partridge being small, well camouflaged and living a rather cryptic life. Observations are usually incidental records but in the course of a year these give a more or less clear picture of partridge presence. Hunters and farmers are sensitised towards the fate of partridges not only because of its – rather former - value as a game bird but also because the grey partridge has always been a popular, charismatic representative of arable landscapes. A combination of rational, social and emotional aspects of the hunters of such agricultural landscapes together with the site confidence of the grey partridge are the main reasons for obtaining satisfactory accuracy for the estimations. Even though the estimations by hunters are not derived from a consistent actively standardised method but rather from an individual process and therefore have a high potential bias it is assumed that a basic degree of standardisation is allowed for by the socio-psychological homogeneity of the respondents. The passive standardisation due to similar interests, similar professions, similar presence phases in the hunting district and a consistent communication culture of the local, rural community explains the highly significant correlation of estimations and ground-truthing partridge densities.

However, it is proposed that the applicability of questionnaire surveys among hunters to gather data on the distribution and population status of other wildlife species has to be evaluated for each considered species as numerous species-specific biases can rule out the usability of such data. Questionnaire surveys are confronted with severe limitations when emotionally negatively documented animals are the focal point (compare Lensing and Joubert 1977, Boshof 1980). Boshof (1980) describes exaggeration yielded from a questionnaire survey among farmers pertaining raptors. For future studies it is recommended to include consideration of the professional, cultural, political background of the respondents and the socio-political situation es-

pecially in respect to the huntability of the grey partridge at the time a questionnaire survey was conducted when such data are analysed.

Standard questionnaires can motivate the involvement of local people in wildlife monitoring and management (Msoffe et al. 2007). An annual survey among hunters such as the WTE on wildlife status and management has the potential of actively involving more “community members” in data collection. By generating data hunters are made aware of underlying problems, for example the reproductive success in the grey partridge in relation to weather conditions or population changes due to changes in the land use system (compare Noss et al. 2005). Hunters are sensitised to the ecology of the partridge and follow the fate of “their” population in their hunting district and in turn as a result of this reflection process often take measures to support partridge populations for example by participating in agri-environmental programs (see Tillmann et al. 2005). Therefore, such an annual questionnaire survey can have in addition to its initial purpose to provide data on the population status of partridges as a basis for decision-making an additionally conservational value for the grey partridge and under the umbrella of its ecological profile for a whole set of species with similar requirements.

The evaluation of the WTE data supports the hypothesis that such a monitoring of the grey partridge provides sufficiently accurate assessments of the status and short-term changes and long-term trends in partridge populations from a regional to federal state level. Its quality is a product of the reliability of the hunters’ estimations combined with the extraordinarily high participation rate of 89.3 % out of 8067 private hunting districts (Strauss 2008).

This questionnaire survey among hunters is a useful monitoring tool for the grey partridge that can not be replaced for example by rule-based habitat models (*sensu* Chamberlain et al. 2004). Such monitoring is vital for detecting population declines, evaluating habitat quality, monitoring conservation action e.g. in the context of agri-environmental measures, monitoring the effect of hunting or carry out environmental impact assessments (compare Bibby et al. 2000, Chamberlain et al. 2004).

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Summary

Ecological profile of the grey partridge

The European arable landscape is becoming increasingly adverse to the survival of “pedestrian” birds like the grey partridge. During the vegetation period, extensively cultivated fields with dense crops fail as habitat for the partridge. The structural depletion of agricultural landscapes and the ensuing loss of diversity in and abundance of arthropods and weeds has led to an overall reduction in resources essential to the partridge; consequently, population densities are now low in the greatest part of its habitat. However, it is possible to optimise agricultural land set aside to reduce agricultural surpluses in the EU or as part of agri-environmental schemes as habitat for the partridge and associated species. In fact, the partridge can be considered typical of a species-diverse, intact agricultural landscape.

Early successional stages of arable land and overwintering stubble fields are known to provide a favourable habitat for the partridge. However, spontaneous regeneration of arable fields can be an agricultural problem because noxious weeds can have an impact both on subsequent use of these fields and on neighbouring fields, particularly in the case of fertile soils.

An agriculturally acceptable alternative is the cultivation of seed mixtures of crops and autochthonic arable plants on set-aside. The choice of plants for the mixture to be sown on such fallow fields should provide heterogeneity of the vegetation on a small scale to form a patchwork, or mosaic, of attractive habitat requisites. To meet the ecological needs of the partridge, patches of bare surface soil should be connected via sparse vegetation to patches of dense vegetation.

Night-time anti-predation and roosting behaviour

Numerous studies focus on the day-time when describing habitat preferences and anti-predation behaviour in the grey partridge (*Perdix perdix*). This is the first study analysing night-time behaviour by means of thermography. In total 640 partridges, clearly avoiding field boundaries as roosting sites to roost in the open field, were observed. Comparing day- and night-time behaviour of partridges they not only perceive a ‘predation risk landscape’ but moreover a ‘predation risk schedule’ resulting in a circadian shift in anti-predation strategies. Furthermore, partridges were ascertained to roost in tighter groupings on darker nights. I hypothesise that the efficiency of visual detection decreases with deteriorating light conditions – confirmed by a de-

creasing flight initiation distance – and partridges huddle closer together fearing such an insecure situation. The preference to roost in smaller subunits within one covey is explained by a more efficient predator detection compared to tight groupings. In contrast to the day-time behaviour, at night the first choice as an escape movement is flying. Altogether partridge behaviour in winter at night was found to be well adapted to predator avoidance and energy economy, explaining the lower predation rates during the ‘covey season’ compared to the spring phases of dispersal, laying and incubation.

Defecation as anti-predation behaviour

Night-time flight behaviour of the grey partridge (*Perdix perdix*) was studied in three agricultural landscapes in Germany in the winter 2005/2006. Thermography was used to detect roosting coveys and record their flight behaviour. Main focus was laid on the analysis of defecation behaviour during the escape flight. With a total of 85 scanning hours 640 partridges in 102 coveys were detected and approached. Flight initiation distance averaged 22.8 m. In at least 75 % of the coveys, defecation occurred upon being flushed. A covey of 15 partridges can produce 60 droppings that appear as a shower on the thermal record distributed over an area of an estimated 200 m².

It is hypothesised that defecation in the context of escape behaviour has various selective advantages besides the reduction of body weight. Predators may be irritated or deterred by excretion of faeces of partridges taking off. As defecation also appears in flushed partridges not being in an immediate life threatening situation this behaviour seems to be uncoupled from parasympathetic reaction of fear. The permanent predator pressure may have selected for a strategic integration of defecation in the escape behaviour of partridges at night.

Evaluation of hunters’ spring pair density estimations

Hunters’ estimations on pair densities of the grey partridge as derived from an annual questionnaire survey (“Game Survey Lower Saxony”, WTE) were evaluated by comparison with detailed ground-truthing censuses in 123 randomly chosen hunting districts representing 63,846.77 ha potential partridge habitat. Estimations and total-census-densities were highly significantly correlated with an average deviation of 24.24%. The discrepancy increased with higher partridge densities and increasing size of the hunting district.

Summary

The satisfactory agreement between the estimations of the hunters – in most cases local farmers - and the direct survey is explained by their comprehensive year-round presence through their hunting, farming but also their leisure activities and their special interest in this charismatic bird combined with the site-confidence of the partridge.

I encourage the consultation of WTE data as a valuable source of basic information on distribution and abundance of partridges to identify spatial conservation priorities, to justify conservation initiatives and to adapt management practices.

Zusammenfassung

Ökologisches Profil des Rebhuhns

Die Art und Intensität der heutigen Landeskultur bieten zumindest großflächig nicht mehr bzw. nur in verringerter Qualität und Quantität die vom Rebhuhn im Laufe seines Lebens benötigten Lebensgrundlagen. Die Lebensraumkapazitäten der heutigen Agrarlandschaft sind, gemessen am ökologischen Anspruch des Rebhuhns, reduziert. Große Schläge mit dichten Feldfruchtbeständen fallen als Lebensraum für den Bodenvogel Rebhuhn aus. Die Struktur- und Artenverarmung der Landschaft hat insgesamt zu einem reduzierten Ressourcenangebot geführt. Das Resultat sind die heute geringen Rebhuhndichten. Im Rahmen von Agrarumweltprogrammen bietet sich die Möglichkeit, Ackerflächen aus der konventionellen Nutzung zu nehmen und als Lebensraum für das Rebhuhn zu optimieren und so die Populationen zu stabilisieren. Dabei kann das Rebhuhn als Repräsentant einer artenreichen Ackerlandschaft gelten.

Es ist bekannt, dass frühe Stadien von Sukzessionsbrachen und Stoppelbrachen zu den beliebtesten Habitattypen des Rebhuhns zählen. Sukzessionsbrachen sind aber auf wüchsigen Standorten landwirtschaftlich problematisch, da dominante Unkräuter zu einer nachhaltigen Beeinträchtigung des Ackerbaus führen können. Das gezielte Ansäen von Kulturpflanzen- und autochthonen Wildpflanzenbeständen bietet eine Alternative.

Die hier diskutierten Ansaatbrachen müssen über ihre Samenmischung und die Bestandsführung ein kleinräumiges Nebeneinander anziehender Lebensraumrequisiten bieten. Bereiche offenen Bodens sollten über schütterere Vegetation hin zu dichter Vegetation überleiten, um den ökologischen Bedarf des Rebhuhns decken.

Nächtliches Feindvermeidungs- und Raumverhalten

Bei der Beschreibung der Habitatpräferenzen und des Feindvermeidungsverhaltens des Rebhuhns fokussieren zahlreiche Untersuchungen auf die Situation am Tag. In der vorliegenden Studie wurde mittels der Thermographie erstmalig das Verhalten bei Nacht erforscht. Insgesamt konnten 640 Rebhühner beobachtet werden, die eindeutig Randstrukturen auswichen, um im offenen Feld zu übernachten. Bei vergleichender Betrachtung von Tag- und Nachtverhalten konnte gezeigt werden, dass Rebhühner nicht nur eine „Prädationsrisiko-Landschaft“, sondern auch einen „Prädationsrisiko-Zeitplan“ wahrnehmen, woraus eine circadiane Verschiebung der An-

tiprädationsstrategien resultiert. Darüber hinaus konnte dokumentiert werden, wie Rebhühner in dunkleren Nächten enger zusammenrücken. Es wird die Hypothese aufgestellt, dass die Effizienz der Feinderkennung in dunkleren Nächten reduziert ist – dies wird durch eine sich entsprechend verringemde Fluchtauslösedistanz bestätigt – und sich die Rebhühner in Anpassung an diese vergleichsweise unsichere Situation enger zusammenfinden. Die bevorzugte Übernachtung in kleinen Untergruppen innerhalb der Rebhuhnkette im Vergleich zu enger Gruppierung sämtlicher Individuen einer Kette wird durch ein dadurch gesteigerte Effizienz früher Feinderkennung erklärt. Im Gegensatz zum Tagverhalten fliehen Rebhühner nachts in erster Linie fliegend. Insgesamt ist festzustellen, dass das nächtliche Verhalten des Rebhuhns eine optimale Anpassung zur Feindvermeidung und Energieeinsparung darstellt. Dies manifestiert sich in niedrigeren Mortalitätsraten während der „Kettensaison“ verglichen mit der Zeit des Dispersals im Frühjahr und während der Balz und Brut.

Defäkation im Feindabwehrverhalten

Das nächtliche Fluchtverhalten des Rebhuhns (*Perdix perdix*) wurde in drei Agrarlandschaften Deutschlands im Winter 2005/2006 untersucht. Thermographisch wurden nächtigende Rebhuhnketten kartiert und ihr Fluchverhalten aufgenommen. Dabei lag der Fokus auf der Dokumentation und Analyse des Defäkationsverhaltens auf dem Fluchtflug. Während insgesamt 85 h thermographischer Kartierung wurden 640 Rebhühner in 102 Ketten detektiert und angegangen. Die Fluchtauslösedistanz betrug im Durchschnitt 22.8 m. Bei mindestens 75 % der auffliegenden Rebhühner kam es zur Defäkation. Eine Rebhuhnkette aus 15 Individuen kann 60 Exkrementportionen abgeben, die auf den thermographischen Aufnahmen wie ein Schauer auf einer Fläche von geschätzten 200 m² niedergehen.

Es wird hypothetisiert, dass dieses Defäkationsverhalten neben der Reduzierung des Start- und Flugwichtes mehrere selektive Vorteile im Fluchverhalten bedingt. Prädatoren könnten durch die während der initialen Fluchtphase abgegebenen Exkremente irritiert und abgeschreckt werden. Da Defäkation auch bei fliehenden Rebhühnern, die sich nicht in einer direkt lebensbedrohlichen Situation befinden, die Regel ist, scheint diese Form der Defäkation von der parasymphatischen Angst-Defäkation evolutiv abgekoppelt zu sein. Der permanente Prädationsdruck könnte eine strategische Integration der Defäkation in das Fluchtverhalten des Rebhuhns bedingt haben.

Evaluierung der Brutbestandschätzungen durch Jäger

Im Rahmen der Wildtiererfassung Niedersachsen (WTE) werden seit 1991 alljährlich sämtliche Jagdrevierinhaber per Fragebogen u. a. zur Situation des Rebhuhns in den von ihnen betreuten Revieren befragt. Um die Einschätzungen der Jäger zur Anzahl der Rebhuhnpaare im Frühjahr in ihrem Revier zu evaluieren, wurden in 123 zufällig ausgewählten Jagdrevieren, die 63.847 ha potentiellen Rebhuhn-Lebensraum repräsentieren, detaillierte Brutpaarkartierungen durchgeführt. Die Schätzungen der Jäger und die Ergebnisse der standardisierten Kartierungen sind hochsignifikant korreliert mit einer durchschnittlichen Abweichung der Schätzungen von den Kartierungsergebnissen von 24,24%. Die Abweichung steigt mit höheren Rebhuhndichten und zunehmender Größe des Jagdreviers.

Die ausreichende Übereinstimmung der Einschätzungen der Jäger, die in den meisten Fällen in der Landwirtschaft tätig waren, mit den Ergebnissen der detaillierten, flächendeckenden Kartierung wird erklärt durch die ganzjährige lokale Präsenz in dem Jagdrevier im Rahmen der landwirtschaftlichen Tätigkeit, der Jagdausübung und anderer Freizeitaktivitäten in der Natur sowie mit dem speziellen Interesse an dem charismatischen Rebhuhn in Kombination mit der Standorttreue des Rebhuhns. Die Verwendung der Daten der WTE als wichtige Basisinformation über die Verbreitung und Abundanz des Rebhuhns wird empfohlen, um räumliche Schutzprioritäten zu identifizieren, Schutzmaßnahmen zu rechtfertigen und Management Methoden anzupassen.

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