Juvenile Survival and Onset of Natal Dispersal in Little Owls (*Athene noctua*) in Relation to Nestling Food Supply

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von

Marco PERRIG

von

Brig-Glis VS

Promotionskomitee

Prof. Dr. Lukas Keller (Vorsitz)

Dr. Beat Naef-Daenzer (Leiter der Dissertation)

Dr. Martin Urs Grüebler

Prof. Dr. Marta Manser

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SUMMARY

Environmental conditions early in life may cause cascading effects through subsequent life-history stages. In birds, the energy supply during growth is a major determinant of nestling survival and physical development. In turn, the fledglings' phenotypic traits may affect survival rates and performance during subsequent life-history stages, including natal dispersal. Latter is a pivotal mechanism in ecology and evolutionary biology. Dispersal is an individual-based process with profound effects on the dynamics, persistence and expansion of populations. However, empirical evidence on natal dispersal and on carry-over effects from conditions during growth beyond the early post-fledging period is scarce. Thus, the determinants of offspring quality and the costs of natal dispersal in relation to growth conditions are unclear. In this thesis I investigate three major subjects: i) the cascading effects of food supply during growth on later life-history stages, ii) stage-specific survival throughout the first year of life and iii) the onset of natal dispersal in relation to age and date.

To study the cascading effects of nestling food supply on later life-history stages, a food supplementation experiment was conducted in a population of little owls (*Athene noctua*). Partial cross-fostering was used to disentangle environmental from intrinsic factors. At fledging, the young little owls were radio-tagged and followed through dispersal until first reproduction. This allowed determining stage-specific survival rates as the major fitness-relevant effect of nestling food supply and gave insights into natal dispersal.

Experimental food supplementation during growth improved nestling survival and affected phenotypic development in a complex way. Supplemented birds were heavier, more likely to accumulate fat deposits, and had longer wings then control owlets. The effects carried over into the post-fledging stage. Specifically, energy stores accumulated during the nestling stage positively influenced post-fledging survival. Experimental food supplementation had no consequences on stage-specific survival rates beyond the post-fledging stage, nor did it affect the timing of the onset of dispersal.

Stage-specific survival rates revealed that the first year of life in little owls was marked by several bottlenecks, differing in the underlying mechanism. About half of the mortality occurred before the onset of dispersal. Variation in food supply during growth was a major predictor of the mortality during this period. The period including natal dispersal composed an important and consistent cost in terms of survival. Part of the mortality during natal dispersal appeared to be related to the roosting behaviour during this period. Individuals roosted less frequently in sheltered sites during the dispersal period compared to other periods. Furthermore, winter survival varied greatly among years, with substantial mortality occurring during periods with a closed snow-cover.

The onset of dispersal of little owls peaked in mid-August, irrespective of the hatching date. Thus, juveniles maximized their time at home rather than starting explorations as soon as possible. The foster family and its environment (i.e. factors acting after the exchange) were more important determinants of the timing of exploratory behaviour beyond the parental territory than factors acting prior to the exchange (including intrinsic factors). However, the mechanism synchronizing the onset of dispersal around mid-August remains unclear.

I draw two main conclusions from this work. First, life-history stages prior to dispersal are crucial for the ecology and population dynamics of little owls. In terms of survival, the most important bottleneck is during the nestling and post-fledging period. Second, trophic relationships are important drivers of little owl ecology. The marked positive effect of experimental food supplementation during growth on pre-dispersal survival rates highlights that food availability has profound effects on the productivity of little owl populations. Food supplemented broods produced about one third more little owls that survived to the first breeding season compared to control broods. However, effects of experimental food supplementation on survival rates only carried over for a short time span beyond the end of the treatment. Similarly, the marked effects of abrupt drops in food availability on winter survival indicate that short-term variation in energy supply has immediate consequences for an individual’s survival prospects. I conclude that survival rates of little owls in their first year of life depend strongly on the temporal and spatial variation in food availability. Little owls are apparently unable to compensate short-term drops in food availability with their own energy reserves. Thus, I suggest that little owls are “income survivors” rather than “capital survivors”.

ZUSAMMENFASSUNG

Die Umweltbedingungen während der ersten Abschnitte des Lebens können sich auf die Kette der nachfolgenden Lebensabschnitte auswirken. Bei Vögeln bestimmt die Energieversorgung während des Wachstums massgeblich das Überleben und die körperliche Entwicklung von Nestlingen. Die phänotypischen Merkmale können sich wiederum auf die Überlebensraten und die Leistungen in späteren Lebensabschnitten, einschliesslich der Abwanderung von Jungtieren, auswirken. Die Abwanderung ihrerseits ist ein zentraler Mechanismus in der Ökologie und der evolutionären Biologie. Sie ist ein Individuen-basierter Prozess mit tiefgreifenden Auswirkungen auf die Dynamik, Beständigkeit und Ausbreitung von Populationen. Trotzdem sind empirische Erkenntnisse zur Abwanderung von Jungtieren spärlich. Ebenso ist schlecht bekannt, wie sich Umweltbedingungen während des Wachstums auf die Zeit nach der Ablösung von den Eltern auswirken. Dementsprechend sind die bestimmenden Faktoren für die Qualität des Nachwuchses und für die Kosten der Abwanderung in Bezug zu den Wachstumsbedingungen unklar. In meiner Dissertation untersuche ich drei Hauptthemen: i) die Kette von Auswirkungen der Nahrungsversorgung während des Wachstums auf spätere Lebensabschnitte, ii) die Überlebensraten in allen Lebensabschnitten im ersten Lebensjahr und iii) den Beginn der Abwanderung in Bezug zum Alter und zum Datum.

Um die Kette von Konsequenzen der Nahrungsversorgung während der Nestlingszeit auf spätere Lebensabschnitte zu untersuchen, wurde ein Zufütterungsexperiment in einer Steinkauzpopulation (*Athene noctua*) durchgeführt. Ein partieller Austausch von Jungtieren half Umweltfaktoren von intrinsischen Faktoren zu unterscheiden. Kurz vor dem Ausfliegen wurden die jungen Steinkäuze mit VHF-Sendern versehen und während der Abwanderung bis zur ersten Fortpflanzung verfolgt. Damit konnten Abschnitt-spezifische Überlebensraten als wichtigste Fitness-relevante Konsequenz der Nahrungsversorgung von Nestlingen bestimmt und Erkenntnisse über die Abwanderung von Jungtieren gewonnen werden.

Die experimentelle Zufütterung während des Wachstums verbesserte die Überlebenschancen der Nestlinge und wirkte sich in komplexer Weise auf die phänotypische Entwicklung aus. Zugefütterte Vögel waren schwerer, hatten häufiger Fettreserven und längere Flügel als Jungtiere der Kontrollgruppe. Die Konsequenzen der Zufütterung reichten auch in die Zeit zwischen dem Ausfliegen und dem Beginn der Abwanderung. Energiereserven, die während der Nestlingszeit angelegt wurden, hatten einen positiven Einfluss auf das Überleben nach dem Ausfliegen. Die experimentelle Zufütterung hatte keine Konsequenzen auf das Überleben nach dem Beginn der Abwanderung oder auf den Zeitpunkt der Abwanderung.

Die Abschnitt-spezifischen Überlebensraten zeigten, dass das erste Lebensjahr von Steinkäuzen durch mehrere „Flaschenhälse" mit relativ hoher Mortalität geprägt war. Etwa die Hälfte aller geschlüpften Jungvögel starb noch vor dem Beginn der Abwanderung. Variation in der Nahrungsversorgung während des Wachstums war ein Hauptprädiktor für die Mortalität während dieser Zeit. Im Zeitabschnitt der Abwanderung waren die Überlebensraten relativ tief. Eine Auswirkung der experimentellen Zufütterung war in diesem Lebensabschnitt nicht nachweisbar. Hingegen schien ein Teil dieser Mortalität im Zusammenhang mit der Schlafplatzwahl während der Abwanderung zu stehen. Während der Abwanderung benutzten junge Steinkäuze seltener geschützte Schlafplätze als in den Lebensabschnitten, in denen sie sesshaft lebten (im elterlichen Wohngebiet, bzw. im eigenen Brutrevier). Das Überleben im Winter variierte stark zwischen den Jahren. Wesentliche Mortalität wurde beobachtet, wenn eine geschlossene Schneedecke lag.

Der Beginn der Abwanderung gipfelte Mitte August, unabhängig vom Schlupfdatum. Demnach maximieren die Jungen eher die Zeit im elterlichen Wohngebiet anstatt so früh wie möglich die Umgebung zu erkunden. Die Pflegefamilie und deren Umfeld (d.h. Faktoren, welche nach dem Tausch wirken) beeinflussten den Zeitpunkt der ersten Erkundungsflüge ausserhalb der elterlichen Territorien stärker als Faktoren, welche vor dem Tausch wirken

(inklusive intrinsische Faktoren). Die Mechanismen, welche den Beginn der Abwanderung um Mitte August synchronisieren bleiben allerdings weitgehend unklar.

Ich ziehe zwei hauptsächliche Schlussfolgerungen. Erstens zeigen die Ergebnisse, dass die Lebensabschnitte vor der Abwanderung für die Ökologie und die Populationsdynamik von Steinkäuzen entscheidend sind. Im Hinblick auf das Überleben liegt der bedeutendste „Flaschenhals“ in der Nestlingszeit und kurz nach dem Ausfliegen. Zweitens sind trophische Zusammenhänge ein wichtiger Faktor in der Ökologie des Steinkauzes. Der deutliche positive Effekt der experimentellen Zufütterung während des Wachstums auf das Überleben vor der Abwanderung unterstreicht, dass das Nahrungsangebot tiefgreifende Auswirkungen auf die Produktivität von Steinkauz-Populationen hat. Insgesamt produzierten die zugefütterten Bruten rund ein Drittel mehr Tiere, die bis zur folgenden Brutsaison überlebten als Kontrollbruten. Allerdings war die Wirkung der Nahrungsversorgung während des Wachstums auf die Überlebensraten nur kurz über das Ende der Zufütterung hinaus nachweisbar. Die deutlichen Folgen abrupter Veränderungen im Nahrungsangebot auf das Überleben im Winter weisen ebenfalls darauf hin, das kurzzeitige Änderungen in der Energieversorgung unmittelbare Auswirkungen auf die Überlebenschancen der Individuen haben. Daher schliesse ich, dass die Überlebensraten von Steinkäuzen im ersten Lebensjahr stark von zeitlichen und örtlichen Unterschieden im Nahrungsangebot bestimmt werden. Steinkäuze vermögen offenbar kaum, kurzfristige Einbrüche in der Nahrungszufuhr durch eigene Energiereserven zu kompensieren.

GENERAL INTRODUCTION

Dispersal is a pivotal mechanism in ecology and evolutionary biology (Bullock *et al.* 2002). It is an individual behavioural strategy, which also has profound effects on the dynamics and persistence of populations. Thus, dispersal links the individual and the population level. In an evolutionary context, dispersal is both subject to selection and a fundamental mechanism maintaining genetic diversity within and between populations (Clobert *et al.* 2001). In contrast to theoretical approaches, empirical research addressing dispersal of individuals within and between populations is scarce and experimental evidence for causal mechanisms is widely lacking.

Dispersal is generally classified into natal and breeding dispersal and involves three successive stages: departure, transience and settlement (Clobert *et al.* 2001; Bowler & Benton 2005). Natal dispersal is the movement from the site of birth to the site of first reproduction, whereas breeding dispersal refers to the movement between subsequent reproductive cycles (Clobert *et al.* 2001). In altricial birds, survival rates after fledging are generally lower compared to the nestling period and after settlement (Maness & Anderson 2013; Cox *et al.* 2014). Thus, much of the selection for important life-history traits is likely to operate between fledging and recruitment, that is, in the period including natal dispersal.

Despite its importance, dispersal (especially the transient stage) is poorly understood due to severe observational problems. Both the ecological mechanisms affecting dispersal and the repercussions on fitness and demographic patterns and processes are unclear (Wiens 2001). All three stages of dispersal may be affected by intrinsic and environmental factors (Clobert *et al.* 2001). For example, dispersal propensity may be genetically determined or may vary in relation to sex (Greenwood 1980; Clarke *et al.* 1997), age, physical condition (Dufty & Belthoff 2001; Forsman *et al.* 2002), personality (Réale *et al.* 2007) and in response to variation in natal habitat quality, such as food availability (Ims & Hjermann 2001), population density (Lambin *et al.* 2001) and predation pressure (Weisser 2001).

The energetic conditions experienced during growth are hypothesized to reach far beyond the termination of parental care (Ims & Hjermann 2001; Bowler & Benton 2005; Benard & McCauley 2008). During growth, a juvenile attains the physical condition and acquires the skills to survive independently. It also gains information on the natal habitat, resource distributions, predation risk and the social environment. In birds, food supply during growth has been shown to have profound effects on the fledglings' phenotypic quality such as body mass, tarsus length, plumage quality and coloration (e.g. Arcese & Smith 1988; Richner 1992; Vergara *et al.* 2010). Furthermore, growth conditions are also supposed to affect individual personality traits and modes to interact with the environment (Dingemanse *et al.* 2004). In turn, these phenotypic traits likely affect an individual's chances to survive later life-history stages and determine behavioural performance after fledging (Naef-Daenzer *et al.* 2001b; Kennedy & Ward 2003; Dingemanse & Réale 2005; Réale *et al.* 2007; Naef-Daenzer & Grüebler 2008). Thus, individuals of good physical condition may have advantages in maintaining their condition and in surviving the presumed risks of dispersal.

Mark-recapture approaches are frequently used to quantify movement rates, but since many individuals are never re-observed, data are often fragmentary, and mortality and dispersal are confounded (Kenward *et al.* 2000). Hence, much of the individual life-history traits, the behavioural and ecological trade-offs and the evolutionary processes shaping dispersal behaviour remain unresolved. Recent advances in tracking technology (Kenward 2001; Naef-Daenzer *et al.* 2001a; Naef-Daenzer *et al.* 2005) opened the way to exploring dispersal patterns and related causal mechanisms in birds. These techniques do not only allow trajectories to be documented but are also the key to estimate survival rates for each stage of the juvenile life-history.

THIS STUDY

This study addresses issues about the cascade of mechanisms that links environmental conditions with phenotypic traits, dispersal behaviour and survival of juvenile birds. In addition to intrinsic factors (such as genotype and maternal effects), environmental factors are considered to affect all three dispersal stages (Ims & Hjermann 2001; Benard & McCauley 2008). While the influence of intrinsic factors has frequently been documented (e.g. differences in dispersal propensity between sexes; Bowler & Benton 2005; for birds: Clarke *et al.* 1997; for mammals: Dobson 1982; Byrom & Krebs 1999), the effects of environmental factors remain largely unknown.

Specifically, this study focuses on the link between food supply during growth and the performance of individuals during subsequent stages. It uses little owls (*Athene noctua*) as a study system. The central question is to what extent food supply affects an individual's phenotypic development and its survival to and during dispersal. An overview of the functional chain of factors that influence the stages of natal dispersal is given in figure 1. An individual's phenotype is shaped by pre-hatching factors (i.e. genetic and maternal effects) and the natal environment. The resulting phenotype in turn may affect departure, transience and settlement either directly or in a cascade through the subsequent dispersal stages. In addition, the natal environment may directly affect the departure decision, irrespective of phenotypic variability.

GENERAL APPROACH

Within this framework, I conducted a field experiment to determine the effects of variation in food supply during growth on survival during later life-history stages and on the onset of dispersal (Fig. 2). The general approach of this experiment was partial cross-fostering of chicks between pairs of simultaneous broods. In addition, one of these broods was food-supplemented during the nestling and early post-fledging period.

To quantify the effect of the experimental treatment on variation in stage-specific survival, survival rates must be estimated for relatively short periods of time (e.g. post-fledging, dispersal, winter) and with high precision. Therefore, large sample sizes and accurate information on the fate of each individual was required to obtain sufficient statistical power. Very high frequency (VHF) radio-telemetry was used to track individuals from fledging to first reproduction and thus, to determine the status (i.e. dead or alive) and location of individuals in short time intervals.

Consequences of the experimental manipulation were expected to cascade through individual life-histories (Fig. 2). Accordingly, **chapter one** presents the effects of the experimental food supplementation on the phenotypic development of nestlings as an important first step in the functional chain. **Chapter two and three** focus on survival rates from fledging to first reproduction in relation to experimental treatment and fledgling phenotypes. **Chapter four** investigates the roosting behaviour of juvenile little owls in relation to life-history stages and environmental conditions. Thus, this chapter investigates a potential explanatory mechanism affecting the costs of natal dispersal. Finally, **chapter five** considers the onset of dispersal behaviour in relation to the experimental treatment and phenotypic traits.

Chapter 1: Fledgling phenotype in relation to nestling food supply

Variation in food intake during growth is assumed to have an effect on an individual’s fate, including dispersal behaviour (Ims & Hjermann 2001; Benard & McCauley 2008). Body condition is the most likely proximate mechanistic link between food supply during growth and dispersal. However, other phenotypic factors (e.g. personality and coloration) may also influence dispersal (Réale *et al.* 2007; Benard & McCauley 2008). In the first chapter of this thesis I investigate the proximate effects of nestling food supply during growth on phenotypic traits of little owl fledglings such as body condition, size, eye coloration and personality.

Hereby, partial cross-fostering allows statistically controlling for intrinsic factors. Thus, chapter one determines important preconditions for subsequent dispersal and for the investigation of carry-over effects of variation in nestling food supply on later life-history stages.

Chapters 2 & 3: Survival rates during the life-history stages from hatching to first breeding in relation to nestling food supply and fledgling phenotype

Current theory considers dispersal to be a costly and risky endeavour (Clobert *et al.* 2001; Bowler & Benton 2005; Benard & McCauley 2008; Johnson *et al.* 2009). Threats and hazards unknown to dispersers may directly decrease survival rates during dispersal compared to the life-history stages preceding and following dispersal. Energetic costs for travelling and resource prospection are also thought to impact survival rates indirectly. Good physical condition prior to departure is thus believed to reduce risks and to have a positive effect on survival throughout dispersal (Witter & Cuthill 1993; Veasey *et al.* 2000). Accordingly, I hypothesized that food supplementation during growth influences survival rates during natal dispersal and other post-fledging life-history stages.

In chapters two and three I determine differential survival rates for each life-history stage from hatching to first reproduction in relation to food supply during growth and to fledgling phenotype. In chapter two I focus on the nestling and post-fledging period (i.e. prior to the onset of dispersal). In chapter three I analyse the period from the onset of dispersal to first reproduction. Thus, these two chapters set the costs of the dispersal stage (in terms of survival) in relation to other life-history stages of the first year of life. Furthermore, the two chapters determine how long potential carry-over effects originating from experimental food supplementation operate.

Chapter 4: Roosting behaviour in relation to life-history stage and environmental conditions

The proximate causes of the costs of dispersal are often unclear. Comparative studies of little owls offer an excellent opportunity to investigate the potential problems faced by dispersers: Within their home-range, little owls frequently use cavities as roosting sites (van Nieuwenhuyse *et al.* 2008). Such sites provide shelter from weather and from predators (e.g. Walsberg 1986; Tillmann 2009), however, they are not easy to find. Tree cavities and entrances to buildings may be inconspicuous. During short stop-over sites, dispersing individuals lack the information on the availability and location of suitable roosting sites. Consequently, dispersers may be more exposed to adverse weather conditions and to predation. In chapter four I investigate the roosting behaviour of little owls before, during and after natal dispersal and in relation to environmental conditions. Thus, the chapter investigates stage-dependent roost site selection as a potential explanatory mechanism affecting the costs (in terms of energy expenditure and predation risk) of natal dispersal.

Chapter 5: The onset of dispersal in relation to nestling food supply and fledgling phenotype

An individual's decision when to disperse is an integral part of the dispersal process. It may have profound consequences for transience, settlement and later life-history stages. Departing individuals face a potential trade-off: leaving early (compared to conspecifics) may be advantageous in acquiring and defending vacant resources (territory holders usually dominate intruders; Alcock 2001), while postponed departure increases the time available within the relative safety of the parental home-range to develop essential skills and to complete growth (Vergara *et al.* 2010). Variation in nestling food supply and related variation in fledgling phenotype potentially result in differential dispersal behaviour. However, the effects of food supply during growth on the onset of dispersal are unclear (Bowler & Benton 2005). In chapter four, I investigate the timing of the onset of dispersal in relation to experimental food supplementation and phenotypic traits at fledging. In this context, the partial cross-fostering allowed estimating the relative importance of factors acting before and after the exchange. The onset of dispersal is characterized by two factors: the age at leaving (i.e. timing in respect to the ontogeny of an individual) and the date of leaving (i.e. timing in respect to the time of the year). I use these factors (i.e. age and date at the onset of dispersal) to test how the beginning of dispersal behaviour is related to individual ontogeny, environmental parameters and the experimental treatment.

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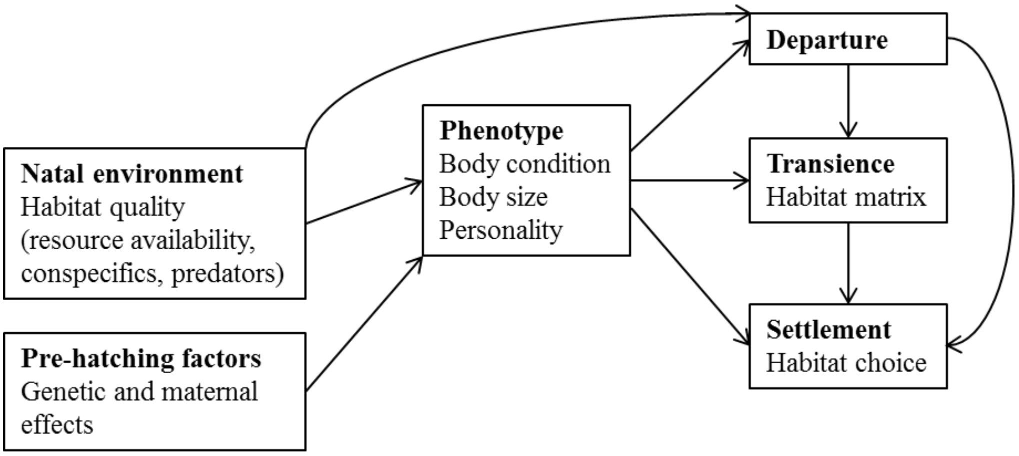

Fig. 1. Simplified scheme depicting the functional chain affecting natal dispersal. The natal environment may directly affect the departure decision, with cascading effects through the three stages of dispersal (departure, transience, settlement). In addition, the natal environment may indirectly affect the dispersal process (and later life-history stages): Phenotypic variation is created by environmental factors of the natal environment and by pre-hatching factors such as genetic and maternal effects. In turn, variation in the phenotype can affect the behaviour during the three stages of dispersal separately as well as the survival probability before, during and after natal dispersal and the reproductive output after settlement. This in turn affects spatial dynamics within and between sub-populations.

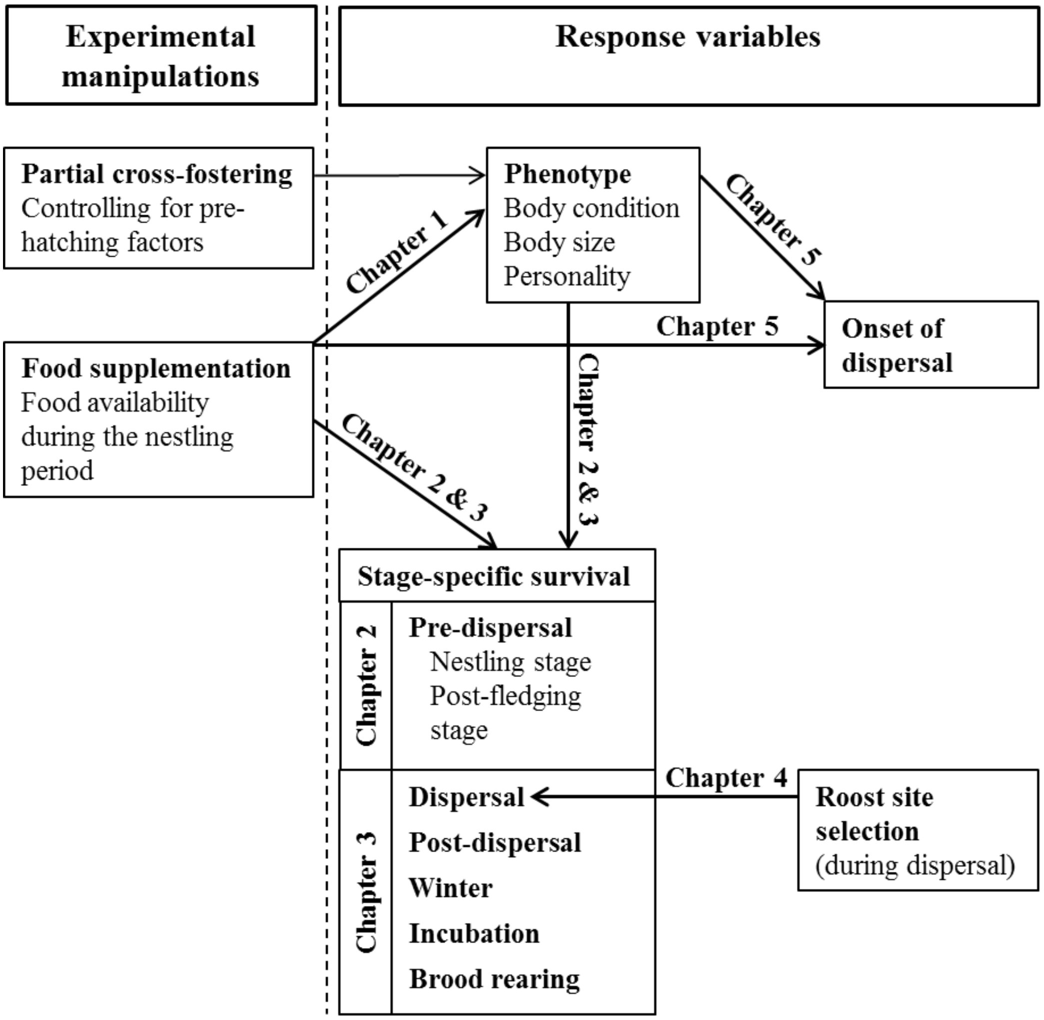

Fig. 2. Schematic representation of the experimental design and the response variables investigated in this thesis. Partial cross-fostering in conjunction with food supplementation allows determining the direct and indirect effects of natal habitat condition on phenotypic variation (Chapter 1), on stage-specific survival rates (Chapters 2 & 3) and on the onset of dispersal (Chapter 5) while controlling for pre-hatching factors.

CHAPTER 1

Experimental food supplementation affects the physical development, behaviour and survival of little owl (*Athene noctua*) nestlings

Marco Perrig, Martin U. Grüebler, Herbert Keil & Beat Naef-Daenzer

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Abstract

In birds, energy supply during growth is a major predictor of the fledglings' physical condition and survival prospects. Differential quantity and quality of fledglings produced under varying nestling food supplies are likely to affect the number of offspring that recruit into the breeding population. However, the underlying mechanisms and associated consequences are still poorly known. Using a partial cross-fostering and food supplementation experiment, we estimated the effect of variation in food supply during growth on nestling survival and fledgling phenotypic traits of little owls (*Athene noctua*). Survival to fledging was much higher in food-supplemented nestlings (98.6%) than in control nestlings (82.4%). Furthermore, supplemented nestlings were on average 8.9 g heavier and were more likely to develop subcutaneous fat deposits (99.4 vs. 73.7% of treatment and control nestlings, respectively). Supplemented nestlings also had on average longer wings than control nestlings, but tarsi and culmen did not differ significantly. Furthermore, experimentally supplemented fledglings struggled more when handled and emerged sooner from tonic immobility than control fledglings. The irises of supplemented fledglings were less intensely coloured. The experimentally induced changes in nestling development probably affect individual performance beyond fledging. Nestlings from orchard-dominated habitats were larger than those from habitats dominated by arable land. As nestling food supply is largely determined by natural food availability, we conclude that habitat quality affects little owl productivity and offspring quality, and ultimately, population dynamics.

Keywords

Eye coloration, fledgling behaviour, fledgling phenotype, nestling energy supply, nestling growth, nestling survival, partial cross-fostering, reproductive success.

Introduction

Energy supply during growth is a major determinant of an individual's physical condition and future reproductive prospects (Lindström 1999). In altricial birds, nestling food supply is determined by natural food availability and parental decisions (Eldegard & Sonerud 2010). The resulting energy flow to the nest affects nestling survival (e.g. Wiehn & Korpimäki 1997; Gonzáles *et al.* 2006; Thorup *et al.* 2010; Wellicome *et al.* 2013) and phenotypic characteristics at fledging. Specifically, augmented energy supply increases fledgling body mass (e.g. Naef-Daenzer & Keller 1999; Hipkiss *et al.* 2002; Santangeli *et al.* 2012) and enhances feather growth (e.g. Berthold 1976; Granbom & Smith 2006) as well as skeletal growth (e.g. Richner 1992; Granbom & Smith 2006; Wellicome *et al.* 2013). In turn, phenotypic traits potentially affect the future performance of independent birds. For example, fledging body mass is a major determinant of post-fledging survival, behavioural performance and recruitment into the breeding population (Verboven & Visser 1998; Naef-Daenzer *et al.* 2001; Naef-Daenzer & Grüebler 2008). Other phenotypic traits such as coloration and behavioural traits govern interactions with conspecifics and the environment, and may signal individual quality (Réale *et al.* 2007; Cote *et al.* 2010; Almasi *et al.* 2012; Wolf & Weissing 2012; Avilés & Parejo 2013). However, the relationships between ecological factors, the expression of phenotypic traits, their proximate influences on individual life-histories and the ultimate consequences on key parameters of population dynamics are poorly understood in most species (Benard & McCauley 2008; Fuller 2012). Understanding the consequences of differential food supply on nestling development is essential to understanding the full effects of natal habitat quality on patterns and processes at the population level.

The populations of many bird species closely associated with agricultural landscapes have declined throughout Europe (Donald *et al.* 2001). Habitat degradation in terms of availability of nesting sites and reduced food resources are believed to be the main causes of population declines (Pain & Pienkowski 1997). Modern agricultural landscapes are characterized by low structural heterogeneity and, consequently, low biodiversity (Pain & Pienkowski 1997). Therefore, agricultural changes may affect the reproductive performance via the mechanisms discussed above.

This study investigated the effect of food supply during growth on nestling survival and phenotypic development in the little owl (*Athene noctua*). The little owl is a characteristic species of agricultural landscapes in Europe (van Nieuwenhuyse *et al.* 2008), with population declines throughout large parts of Europe over the past three decades (van Nieuwenhuyse *et al.* 2008). Reduced food availability as a consequence of habitat degradation is regarded as one of the main causes of poor reproductive success across Europe (van Nieuwenhuyse *et al.* 2008). However, the effects of food supply during the nestling phase on phenotypic development and nestling survival are unclear. Under the general assumption that an increase in food supply enhances nestling development and reduces sibling competition (Mock *et al.* 1990; Drummond 2001), we predicted that experimental food supplementation during the nestling phase would improve nestling survival and affect nestling phenotype and behaviour. Specifically, we predicted that food supplementation would increase body mass and fat deposition, enhance structural growth (i.e. skeleton and plumage) and affect individual behaviour.

Materials and methods

The study was conducted in a little owl sub-population of approximately 220 breeding pairs in southern Germany (Landkreis Ludwigsburg, Baden-Württemberg, 48°53’43″N, 9°11’45″E). Since 1988 the breeding success of the entire sub-population has been monitored (H. Keil unpubl. data). For this study, 124 broods with 414 hatchlings were closely monitored during the four breeding seasons from 2009 to 2012.

EXPERIMENTAL DESIGN

To quantify the effects of variation in food supply we conducted a partial cross-fostering and food supplementation field experiment. Partial cross-fostering allowed supplementing only some nestlings from the same family. Thus, intrinsic factors acting on survival and phenotypic development could be statistically controlled for. Two synchronous broods were denoted as partner broods. One of the two was randomly assigned to experimental treatment (i.e. food supplementation). Depending on brood size, one or two nestlings of similar age and body weight were exchanged among partner broods, keeping brood sizes constant. Exchange took place at c. 14 days of age. Conservation concerns prohibited earlier manipulation of nestlings. Food supplementation started after exchange. All broods were visited every second day for 36 days. Thus, visits continued beyond fledging at c. 30 days of age, when nestlings leave the nestbox for the first time. After fledging, juvenile little owls stay within close proximity of and regularly return to the nestbox. During visits a total of 480 g of dead laboratory mice per nestling was deposited inside the nestbox of supplemented broods, 20 g per visit and nestling for the first six visits, 30 g per visit and nestling thereafter. Food supplementation represented a c. 40% increase in food compared with natural food supply (Juillard 1984).

This study aimed to determine the effects of nestling food supply while controlling for potential confounding effects, hence the use of cross-fostering to control for intrinsic factors. In 2010 and 2011, a total of 56 broods were subjected to the full experiment (i.e. partial cross-fostering and food supplementation, Table 1). In addition, 68 broods not subjected to partial cross-fostering were included better to estimate the effect of food supplementation (49 control broods and 19 supplemented broods, Table 1). No treatment was performed in 2009.

DATA COLLECTION

The hatching date of each nestling was determined using developmental illustrations (van Nieuwenhuyse *et al.* 2008) and the equations given in Juillard (1979). Owlets were measured at the ages of 13.7 ± 5.57 days (mean ± 1 SD, n = 267, hereafter first measurement), 21.5 ± 3.99 days (n = 345, second measurement) and 29.4 ± 3.29 days (n = 307, third measurement). To minimize disturbances across the population, the first measurement was only taken in broods handled anyway during partial cross-fostering. Plastic colour rings were used to identify individuals prior to ringing. At each measurement body mass (to the nearest 0.1 g), and the lengths of the wing and of the ninth primary (to the nearest 0.5 mm), as well as of the tarsus and the culmen (to the nearest 0.1 mm) were recorded.

At the third measurement, feather samples were obtained for genetic sex determination of the nestlings, and the presence or absence of fat deposits under the wing was recorded. Growth conditions may also affect appearance (e.g. eye colour) and behaviour. Both have the potential to affect later life-history stages (Bortolotti *et al.* 2003; Duckworth & Badyaev 2007; Duckworth 2008; Guillemain *et al.* 2012). Thus, we recorded eye coloration (i.e. pale or intense as compared with reference photographs) as one trait of individual appearance that has potential signalling functions (Guillemain *et al.* 2012). Additionally, we recorded the owlets' behaviour during handling (i.e. passive or struggling) and conducted a tonic immobility (TI) test (Forkman *et al.* 2007). To induce TI, an owlet was held on its back for 10 s. Upon release, time until righting of the animal was recorded. If this time was less than 10 s in three consecutive trials, TI was classified as 'not induced'. The TI test was terminated 290 s after release. Individuals that failed to get up during the experiment were assigned a TI time of 290 s (n = 34).

Hatching asynchrony within a brood leads to a developmental gradient among siblings (van Nieuwenhuyse *et al.* 2008). When food is limited, this gradient benefits early-hatched nestlings in sibling competition (Mock 1985). To include this developmental gradient, a developmental rank was assigned to each nestling according to the estimated hatching date. The oldest nestlings in a brood were assigned a rank of zero. Nest mates were assigned the same rank if the estimated age difference was smaller than days. Because the developmental rank of a nestling may change during the nestling phase (e.g. when a sibling dies), the developmental rank was adjusted at each measurement.

Each measurement was assigned a label 'family history' combining the individual's original family and its family at measurement. For example, the first measurement of a nestling that hatched in family 'A' but was later exchanged to family 'B' was labelled 'A A'. The second and third measurements of the same nestling (i.e. after the exchange) were labelled 'A B'. Thus, this factor accounted for the exchange, representing the original as well as the foster family.

Due to missing data, sample sizes differed between analyses of dependent variables (Table 2).

ANALYSIS OF MORPHOLOGICAL PARAMETERS

The effect of food supplementation on morphological parameters (i.e. body mass, length of wing, tarsus and culmen) was analysed using linear mixed effects models with the package arm (Gelman & Su 2013) in the statistical software R 3.0.2 64-bit (R Core Team 2013). Morphological parameters were separately modelled as a function of nestling age with treatment as a fixed factor. The maximal model included fixed effects to control for the developmental rank, for brood size at measurement and for hatching date. Polynomial factors were included for age (cubic) and hatching date (quadratic) to approximate the non-linear nature of nestling growth and environmental conditions throughout the year. The individual and family history were included as random factors to account for individual dependency and individual history, respectively. Year was also included as a random factor. The maximal model further included two-way interactions between food supplementation and fixed factors.

Backwards model selection according to the Bayesian Information Criterion (BIC) was used to remove non-significant interactions (Burnham & Anderson 2002). To facilitate model convergence, orthogonal polynomials of age and hatching date were used and all covariates were standardized (mean = 0, SD = 1). Residuals of the maximal model were inspected to confirm model assumptions. Ninety-five per cent credible intervals (CrI) for all fixed and random factors were obtained from the simulated posterior distribution (5000 simulations). As some individuals were not sexed (Table 2), the effect of sex as a fixed effect was determined post-hoc on a reduced dataset (using the CrI from 5000 simulations).

ANALYSIS OF BINOMIAL VARIABLES

Binomial response variables (i.e. presence/absence of fat deposits under the wing, passive/struggling behaviour during handling, pale/intense eye coloration) were analysed with generalized linear mixed effects models assuming a binomial distribution of the residuals with the package arm (Gelman & Su 2013) in R 3.0.2 64-bit (R Core Team 2013). The analytical approach was identical to the analysis of morphological parameters, but the maximal model was adjusted to the specific characteristics of the data. As only a single measurement per individual was taken, no random factor for the individual was included. Datasets were reduced to measurements at ages from 25 to 30 days. As a consequence, age was only included as a linear fixed factor.

ANALYSIS OF NESTLING SURVIVAL

Nestling survival was defined as survival from hatching to day 30 post-hatching. Analysis of nestling survival was identical to the analysis of binomial variables, except that nestling age was excluded from the analysis. As animals were only sexed shortly before fledging (i.e. after nestling mortality has occurred), no post-hoc test for the effect of sex on survival was conducted.

ANALYSIS OF TONIC IMMOBILITY

Factors affecting the duration of TI were analysed using Cox proportional hazards models with random effect with the package coxme (Therneau 2012) in R 3.0.2 64-bit (R Core Team 2013). The analytical approach was identical to the analysis of morphological parameters (i.e. backwards model selection according to the BIC, use of orthogonal polynomials and standardization of covariates). The maximal model was based on the maximal model of binomial variables. As the experimenter has a marked effect on the TI test (Forkman *et al.* 2007), the experimenter was included as a random effect in the maximal model. Model interferences were based on the score test statistics at a significance level of 0.05.

EFFECTS OF ENVIRONMENTAL FACTORS

Nestling food supply is ultimately driven by natural food availability. Thus, experimental food supplementation simulates an improvement in habitat quality in terms of food availability. As the availability of food varies among territories and over time, we expected nestling survival and development to vary in relation to environmental factors that are linked to natural food sources. Based on the models used to calculate the effect of food supplementation, we performed a post-hoc test for the interaction between food supplementation and the random effect year, and for differences between broods reared in different habitats as a fixed effect (i.e. habitats dominated by arable land vs. orchard-dominated habitats).

The 95% CrI of the posterior distribution (5000 simulations) was used to determine the significance of fixed factors. Because the CrI does not allow for significance testing of random effects, the BIC was used to test the treatment–year interactions (Burnham & Anderson 2002).

Results

BODY CONDITION

On average, food-supplemented nestlings were 8.9 g (CrI = 6.0 – 11.8 g) heavier than control nestlings (Table 3a, Fig. 1a). Compared with the average body mass of control nestlings between ages of 26 and 35 days (133.6 g, $n = 200$) this corresponded to an increase of 6.7%. In addition, virtually all supplemented nestlings had subcutaneous fat deposits under the wing ($P_{\text{treatment}} = 0.994$, CrI = 0.955 – 0.999; Fig. 2a), whereas fat was observed in fewer than three-quarters of the control nestlings ($P_{\text{control}} = 0.737$, CrI = 0.201 – 0.967; Fig. 2a).

Factors other than experimental treatment substantially affected the body condition (taken as body mass and fat deposits, both integral parts of body condition) of little owl fledglings. The growth curve of body mass showed the typical rapid growth during the nestling phase reaching an asymptote around fledging at c. 30 days (Fig. 1a). Furthermore, body condition varied with hatching date. Nestlings hatched late in the breeding season grew heavier than nestlings hatched early in the season (Table 3a). In contrast, nestlings hatched early and late in the breeding season were more likely to have subcutaneous fat stores than birds hatched mid-season (Table 3a). Within broods, the developmental rank of the owlets also affected body mass. Lower-ranked (i.e. earlier-hatched) nest mates grew heavier than higher-ranked nest mates (Fig. 3a). Brood size had no effect on body condition (Table 3a). Model selection under the BIC revealed no significant interaction and the post-hoc tests revealed no effect of sex on body condition (Table 4).

STRUCTURAL GROWTH

On average, the wings of supplemented nestlings were 4.4 mm (CrI = 3.0 – 5.7 mm) longer than those of control birds (Table 3b, Fig. 1b). Compared with the average wing length of control nestlings between ages of 26 and 35 days (110.1 mm, $n = 131$) this corresponded to an increase of 4.0%. The increase of 0.4 mm (CrI = -0.03 to 0.79 mm) in tarsus length and 0.1

mm (CrI = -0.01 to 0.22 mm) in culmen length due to food supplementation was not significant (Table 3b, Fig. 1c, d). Compared with the average tarsus and culmen length of control nestlings between ages of 26 and 35 days (tarsus: 35.0 mm, n = 182; culmen: 12.8 mm, n = 171) this corresponded to an increase of 1.1 and 0.8%, respectively.

Structural growth was also related to factors other than food supplementation. As with body mass, the pattern of structural growth was primarily related to nestling age. Structural growth was most pronounced during the nestling period and approached an asymptote after 30 days for tarsus and culmen, somewhat later for wing (Fig. 1b–d). Furthermore, advancing breeding season positively affected structural growth (Table 3b). Little owls hatching at the end of May grew approximately 8 mm longer wings, 1 mm longer tarsi and 0.5 mm longer culmen than those hatching at the end of April. For wing growth, this seasonal effect decreased towards the end of the breeding season (Table 3b). In addition, lower-ranked (i.e. earlier-hatched) nest mates grew longer tarsi than higher-ranked nest mates (Fig. 3b) and larger broods produced larger nestlings in terms of skeletal growth (Table 3b). The effect of food supplementation on the size of wing and tarsus was more pronounced in small broods than in large broods (Table 3b). Post-hoc tests revealed no effect of sex on structural growth (Table 4).

NESTLING SURVIVAL

Almost all supplemented nestlings survived the first 30 days after hatching ($P_{\text{treatment}}$ = 0.986, CrI = 0.945 – 0.997). In contrast, 17.6% of the control owlets died as nestlings (P_{control} = 0.824, CrI = 0.717 – 0.896; Fig. 2b). Survival of non-supplemented nestlings improved with advancing breeding season and thus the effect of food supplementation declined with advancing season (Fig. 4). Within control broods, nestling survival was strongly related to the developmental rank. Within broods of large hatching asynchrony, the first-hatched (i.e. lowest-ranked) nestlings had a nine-fold higher survival probability compared with last-hatched nestlings (Fig. 3c). Food supplementation virtually eliminated this effect. This indicates that the youngest nest mates within a brood profited most from experimental food supplementation. Brood size had no significant effect on nestling survival (Table 3c).

BEHAVIOURAL TRAITS

Compared with control nestlings, a higher proportion of supplemented nestlings struggled when handled ($P_{\text{treatment}}$ = 0.864, CrI = 0.680 – 0.951; P_{control} = 0.626, CrI = 0.246 – 0.901; Fig. 2c). Supplemented nestlings also emerged on average 14.8 s sooner from tonic immobility ($P = 0.035$).

Behavioural traits were also related to factors other than experimental food supplementation. The probability of a nestling struggling during handling increased with nestling age (Table 3d) and with increasing developmental rank (Table 3d, Fig. 3d). Furthermore, time to emergence from TI decreased over the course of the breeding season (Table 3d). Brood size did not affect countenance during handling or TI time (Table 3d). For behavioural traits, model selection under the BIC revealed no significant interaction and the post-hoc tests for sex were not significant (Table 4).

EYE COLORATION

Compared with control nestlings, a significantly lower proportion of supplemented nestlings had intensively coloured eyes ($P_{\text{treatment}}$ = 0.617, CrI = 0.344 – 0.829; P_{control} = 0.830, CrI = 0.633 – 0.934; Fig. 2d). Hatching date was the only factor besides experimental treatment affecting eye coloration (Table 3e). The probability that nestlings had intensively coloured eyes increased over the course of the season. Model selection under the BIC revealed no significant interaction for eye coloration and the post-hoc test revealed no effect of sex on eye coloration (Table 4).

EFFECTS OF ENVIRONMENTAL FACTORS

For all dependent variables the interactions between food supplementation and year were not significant according to the BIC ($\Delta BIC = BIC_{without\ interaction} - BIC_{with\ interaction}$ for TI = 0.00, ΔBIC for all other tested variables < -10; $\Delta BIC > 2$ is considered significant).

Across the entire dataset and controlling for experimental effects, little owl nestlings growing up in orchard-dominated habitats were significantly heavier (4.94 g, CrI = 0.09 – 10.09 g) and larger in terms of wing length (2.55 mm, CrI = 0.18 – 4.83 mm) and tarsus length (0.77 mm, CrI = 0.15 – 1.41 mm) than were nestlings growing up in habitats dominated by arable land.

Discussion

Food supplementation experiments have frequently been used to determine the effects of energy supply during different phases of the reproductive cycle (Martin 1987) and often show that sufficient food supply during early development is crucial for the fledgling's physical condition and survival prospects (e.g. Dewey & Kennedy 2001; Thorup *et al.* 2010; Wellicome *et al.* 2013). In our study, experimental food supplementation strongly increased little owl survival from hatching to fledging and profoundly altered the nestlings' physical and behavioural development. Supplemented nestlings accumulated substantial subcutaneous fat stores, and fledged heavier and with longer wings. Their eyes were paler, potentially affecting the signalling function of eyes (e.g. Guillemain *et al.* 2012). Supplemented nestlings also struggled more when handled and emerged faster from tonic immobility. Thus, increasing nestling food supply substantially affected two major aspects of reproductive success: the survival of nestlings to fledging and the quality of fledglings.

The clear effects of the flow of energy to little owl broods are ultimately driven by natural variation in food availability. Our results highlight that control broods grew below the maximal physiological rate, suggesting that parents did not fully compensate for environmental variation in food availability. Thus, spatial and temporal variation in food availability is expected to cause spatial and temporal variation in offspring survival and quality. Rodents are a major food source of little owls in Central Europe (van Nieuwenhuyse *et al.* 2008). Orchards, extensive grassland, pasture and edge structures sustain high rodent densities, whereas mechanically cultivated fields are virtually rodent-free (Apolloni 2013). The results of this study match this pattern; little owl territories encompassing a large proportion of orchards and grassland produced larger fledglings (in terms of body mass, wing and tarsus) compared with territories dominated by arable land. On the temporal scale, live trapping data from 2010–2012 (own unpubl. data) indicated that rodent density increased in each year from spring to summer. This may explain the findings that little owl nestlings hatched in June were larger (in terms of body mass, wing, tarsus and culmen) and emerged earlier from TI than nestlings hatched in May. Also, June hatchlings were more likely to survive the nestling phase. We conclude that spatio-temporal patterns of natural food availability directly translate into variation in the productivity and offspring quality of little owl broods to an extent similar to the results of the experimental supplementation.

The flow of energy to nestlings is also mediated through parental performance and decisions. Parents face a trade-off in energy allocation between current and future reproduction (Eldegard & Sonerud 2010; Santangeli *et al.* 2012) and this may provide an explanation for control broods not developing at maximum rates. From a parental perspective, the related reduction in numbers and quality of the current brood may be outweighed by the long-term allocation of parental resources to subsequent reproductive attempts.

HATCHING ORDER AND FOOD SUPPLEMENTATION

The hatching order within a brood also had marked effects on nestling survival and development. First-hatched nestlings grew larger (in terms of tarsal length) and heavier, struggled less when handled and had much better chances of surviving the nestling phase. The difference in physical development between the first- and the last-hatched owlet in a brood with high hatching asynchrony was even larger than the average effect size of the treatment. The survival rates of the highest-ranked owlets were particularly low and strongly increased with food supplementation. Accordingly, within broods, last-hatched nestlings profited most from food supplementation, which increased the overall fledging success of the brood. The likely mechanism behind improved survival of late-hatched nestlings is therefore that food supplementation reduced competition among siblings, which in turn mitigated brood reduction (for reviews of the brood reduction hypothesis see Mock *et al.* 1990; Drummond 2001).

EFFECTS BEYOND FLEDGING

While the consequences of increased nestling survival on reproductive success and, in turn, on demographic parameters are straightforward, the effects of fledgling phenotypic traits on post-fledging performance and future reproductive success are not. There is evidence that some phenotypic traits at fledging influence the performance of independent birds. For example, body mass at fledging was correlated with post-fledging home-range size, short-term movements and survival, and with the potential to recruit into the breeding population (Simons & Martin 1990; Both *et al.* 1999; Naef-Daenzer *et al.* 2001; Monròs *et al.* 2002; Naef-Daenzer & Grüebler 2008). For other phenotypic traits the consequences are still controversial. For example, avian fat stores are important energy reserves, but also increase emergency take-off time (Witter & Cuthill 1993). Thus, fat stores may improve or decrease post-fledging survival.

CONCLUSIONS

Two main conclusions emerge from our results. First, variation in nestling food supply leads to differential nestling survival and differential physical and behavioural development.

Therefore, the proximate effect of increasing the flow of energy to the brood is to increase the number of fledging offspring and alter their quality. These findings contribute to explaining the seasonal, annual and spatial variation in fecundity documented in little owl populations (van Nieuwenhuyse *et al.* 2008). Secondly, the results suggest that the cascade of mechanisms that links habitat characteristics to reproductive output and offspring quality may have further consequences for key parameters of demography. The trophic conditions during early development probably carry over to post-fledging survival, dispersal movements and recruitment. Consequently, full comprehension of the chain of mechanisms determining reproductive performance and offspring survival contributes to clarifying the ecological processes that cause the declines in farmland species such as the little owl. From a wider perspective, our results underline that agricultural impacts at spatial and trophic levels strongly affect the reproductive performance of species and thus the biodiversity of agricultural landscapes. Accordingly, conservation measures to optimize habitat quality and food resources may strongly support the productivity of local populations.

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Table 1. Number of control and experimentally supplemented (i.e. treatment) broods across years. Broods involved in partial cross-fostering are listed separately from broods not involved in partial cross-fostering. The total number of nestlings exchanged in each year is given in the last column.

	Year	Control broods	Treatment broods	Exchanged nestlings
Cross-fostered	2010	14	14	54
	2011	14	14	50
Not cross-fostered	2009	13	0	-
	2010	4	0	-
	2011	16	3	-
	2012	16	16	-
Total		77	47	104

Table 2. Sample sizes for the analyses of different parameters. The two numbers in the last column indicate the number of observations/number of individuals with unknown sex, respectively.

Analysed Parameter	Observations	Individuals	Family history	Year	Sex unknown
Body mass	936	389	173	4	92 / 68
Wing	635	324	154	3	54 / 47
Tarsus	877	384	173	4	81 / 63
Culmen	875	385	173	4	82 / 64
Fat deposits	215	215	116	3	4 / 4
Countenance	199	199	111	3	1 / 1
Eye colour	179	179	99	3	1 / 1
Tonic immobility	231	231	129	3	1 / 1
Survival	414	414	181	4	93 / 93

Table 3. Parameter estimates (and 95% CrI of the posterior distribution) of the nine models run for the different response variables: (a) body condition (i.e. body mass and fat), (b) structural growth (wing, tarsus and culmen), (c) survival, (d) behaviour (countenance, tonic immobility) and (e) eye colour. For tonic immobility exp (coef), standard deviations (coef) and *P*-values are given for the fixed factors. Standard deviations are given for random effects. Significant fixed effects according to the 95% CrI are marked with asterisks. Orthogonal polynomials were constructed and all covariates were standardized (mean = 0, SD = 1) prior to analysis. Sample sizes are given in Table 2.

	(a) Body condition					
	Body mass			Fat		
Fixed factors	Estimate	95% CrI		Estimate	95% CrI	
Treatment	8.88*	6.04	11.81	4.13*	2.02	6.26
Age	23.18*	22.07	24.24	0.01	-0.67	0.67
Age^2	-9.68*	-10.51	-8.84	-	-	-
Age^3	2.70*	1.88	3.50	-	-	-
Hatching date	2.09*	0.36	3.90	0.04	-0.89	0.98
Hatching date^2	-0.26	-2.13	1.62	1.12*	0.02	2.22
Brood size	0.11	-1.51	1.74	-0.20	-1.07	0.66
Developmental rank	-2.08*	-3.10	-1.07	-0.53	-1.18	0.12
Intercept	113.12*	109.85	116.38	1.03	-1.38	3.38
Random factors	SD			SD		
Year	3.13			1.90		
Family history	10.31			2.69		
Individual	4.88			-		
Residuals	9.69			-		

Table 3. (*continued*)

	(b) Structural growth									**(c)** Survival		
	Wing length			Tarsus length			Culmen length			Survival		
Fixed factors	Estimate	95% CrI		Estimate	95% CrI		Estimate	95% CrI		Estimate	95% CrI	
Treatment	4.35*	3.00	5.68	0.39	-0.03	0.79	0.10	-0.01	0.23	2.72*	1.31	4.11
Age	35.80*	35.22	36.39	4.57*	4.41	4.73	1.39*	1.35	1.44	-	-	-
Age^2	-1.15*	-1.65	-0.67	-1.68*	-1.81	-1.54	-0.35*	-0.39	-0.31	-	-	-
Age^3	-2.80*	-3.25	-2.36	0.38*	0.25	0.51	0.05*	0.01	0.08	-	-	-
Hatching date	1.57*	0.72	2.40	0.28*	0.06	0.51	0.07*	0.01	0.14	1.05*	0.14	1.96
Hatching date^2	-0.82*	-1.64	-0.01	-0.06	-0.29	0.17	-0.06	-0.13	0.01	0.60	-0.37	1.61
Brood size	0.68	-0.13	1.48	0.79*	0.56	1.04	0.08*	0.02	0.15	0.04	-0.46	0.56
Developmental rank	0.26	-0.21	0.74	-0.21*	-0.37	-0.06	-0.01	-0.06	0.04	-0.77*	-1.15	-0.39
Treatment x brood size	-2.34*	-3.50	-1.14	-0.86*	-1.25	-0.46	-	-	-	-	-	-
Treatment x hatching date	-	-	-	-	-	-	-	-	-	-2.25*	-4.09	-0.48
Intercept	76.01*	75.09	76.95	31.11*	30.28	31.96	11.54*	11.37	11.71	1.55*	0.93	2.15
Random factors	SD			SD			SD			SD		
Year	0.00			0.94			0.20			0.00		
Family history	4.16			1.16			0.30			2.19		
Individual	1.76			0.52			0.27			-		
Residuals	4.17			1.66			0.47			-		

Table 3. (*continued*)

	(d) Behaviour						**(e)** Eye colour		
	Countenance			Tonic immobility			Eye colour		
Fixed factors	Estimate	95% CrI		exp (coef)	SE (coef)	*P*	Estimate	95% CrI	
Treatment	1.33*	0.24	2.44	1.49*	0.19	0.035	-1.11*	-2.23	-0.00
Age	0.54*	0.04	1.03	0.99	0.11	0.910	0.08	-0.47	0.61
Hatching date	-0.23	-0.75	0.30	1.25*	0.10	0.021	0.60*	0.00	1.21
Hatching date^2	0.19	-0.31	0.70	1.10	0.10	0.310	-0.44	-1.03	0.16
Brood size	-0.40	-1.03	0.19	0.91	0.11	0.390	0.06	-0.53	0.64
Developmental rank	0.54*	0.02	1.03	1.05	0.08	0.590	-0.37	-0.86	0.11
Intercept	0.51	-1.12	2.21	-	-	-	1.58*	0.55	2.64
Random factors	SD			SD			SD		
Year	1.31			0.02			0.50		
Family history	1.67			0.47			1.68		
Experimenter	-			0.39			-		

Table 4. Post-hoc tests for sex. Estimates for the factor sex (males), the 95% CrI from the posterior distribution, ΔBIC ($\text{BIC}_{\text{without sex}} - \text{BIC}_{\text{with sex}}$), and sample sizes are given. A ΔBIC > 2 is considered significant. For tonic immobility the exp (coeff) is given instead of the estimate.

Response variable	Estimate	95% CrI		ΔBIC	Observations	Individuals	Background	Year
Body mass	0.78	-1.02	2.56	-6.03	844	321	164	4
Wing	0.47	-0.52	1.44	-5.48	581	277	150	3
Tarsus	-0.03	-0.34	0.28	-6.64	796	321	164	4
Culmen	0.10	-0.00	0.20	-2.72	793	321	164	4
Fat deposits	-0.05	-1.09	1.01	-5.60	211	-	116	3
Countenance	-0.28	-1.19	0.62	-4.96	198	-	111	3
Tonic immobility	1.15	-	-	-4.53	230	-	128	3
Eye colour	0.28	-0.62	1.17	-4.88	178	-	98	3

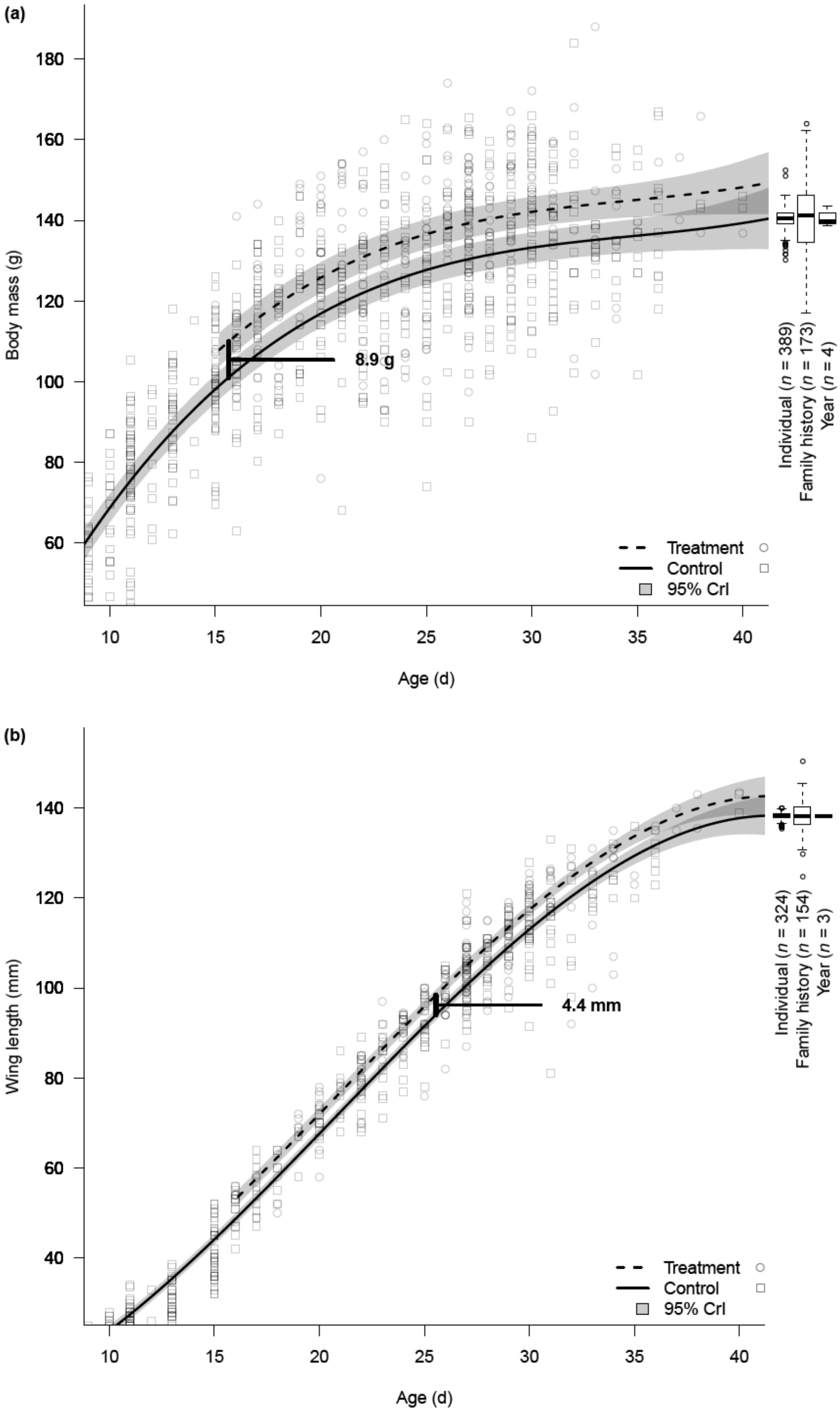

Fig. 1. Growth curves of food-supplemented (dashed line) and control (solid line) nestlings for (a) body mass, (b) wing length, (c) tarsus length and (d) culmen length. Open circles and squares represent measurements of food-supplemented and control owlets, respectively. Ninety-five per cent CrI from the posterior distribution are shaded in grey. Boxplots represent model outputs for the random effects. Sample sizes are given in Table 2.

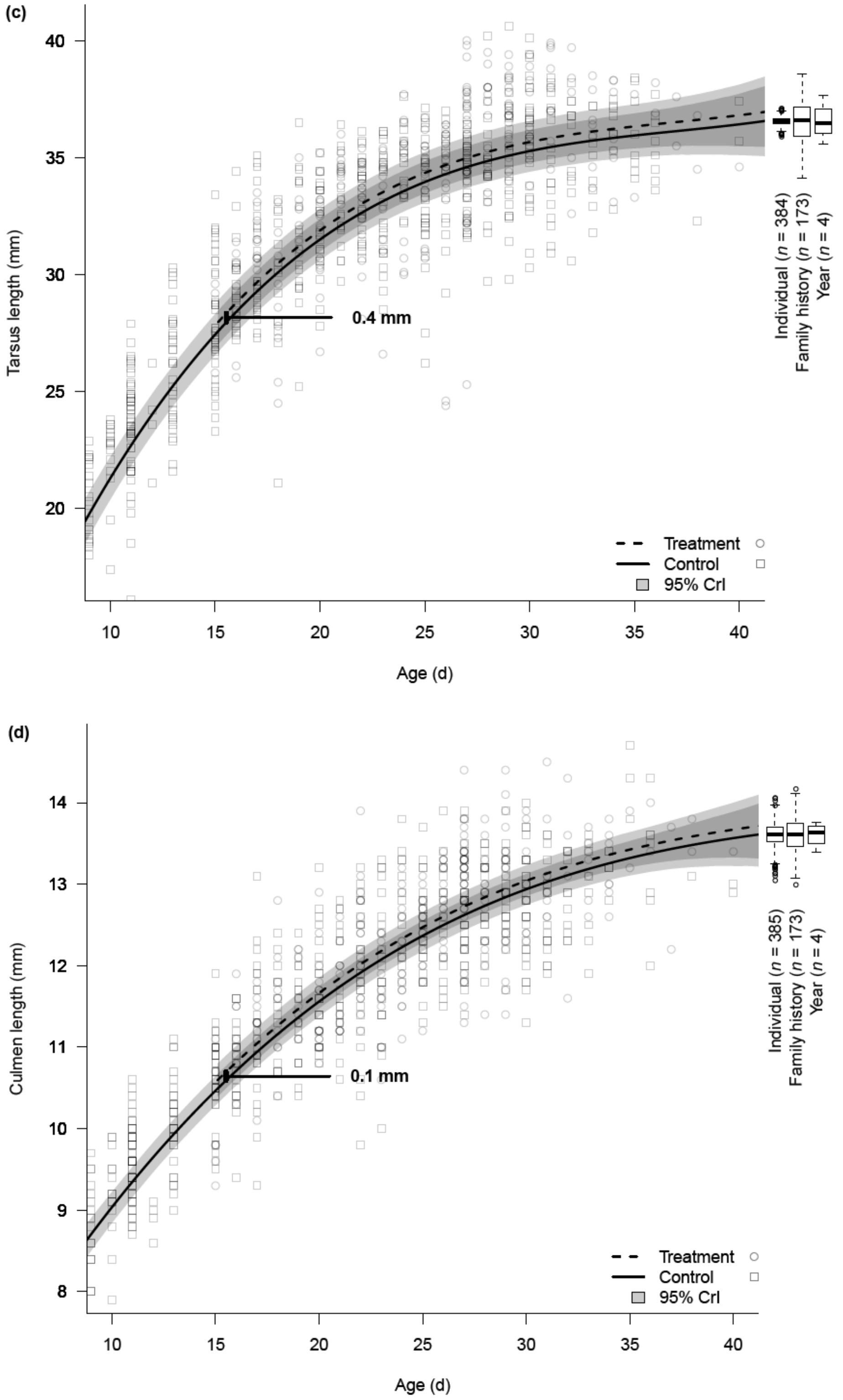

Fig. 1. (*continued*)

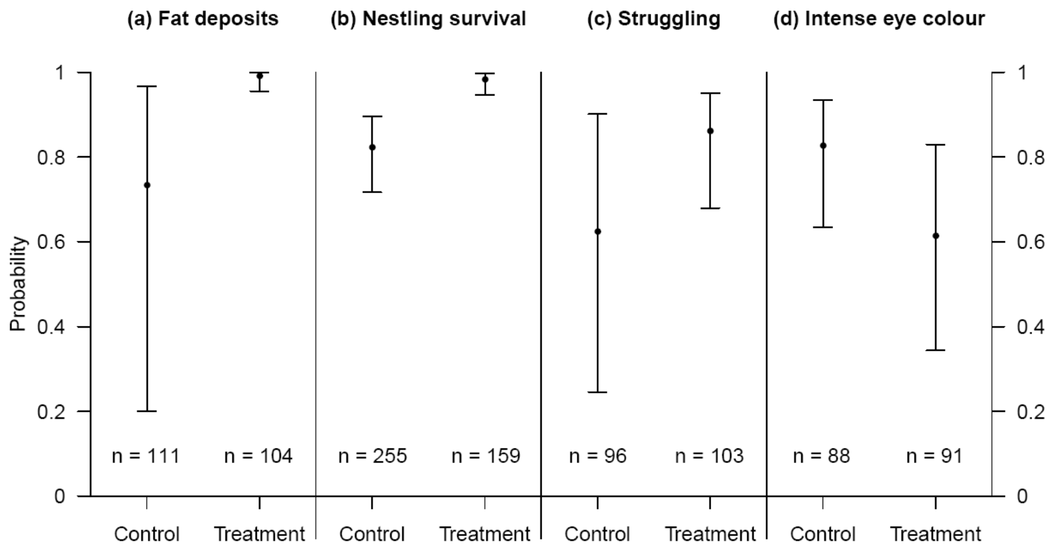

Fig. 2. Effects of food supplementation on the probability of (a) having subcutaneous fat deposits under the wing, (b) surviving the nestling phase, (c) struggling when handled and (d) having intense eye coloration in little owl nestlings. Error bars indicate the 95% CrI of the posterior distribution.

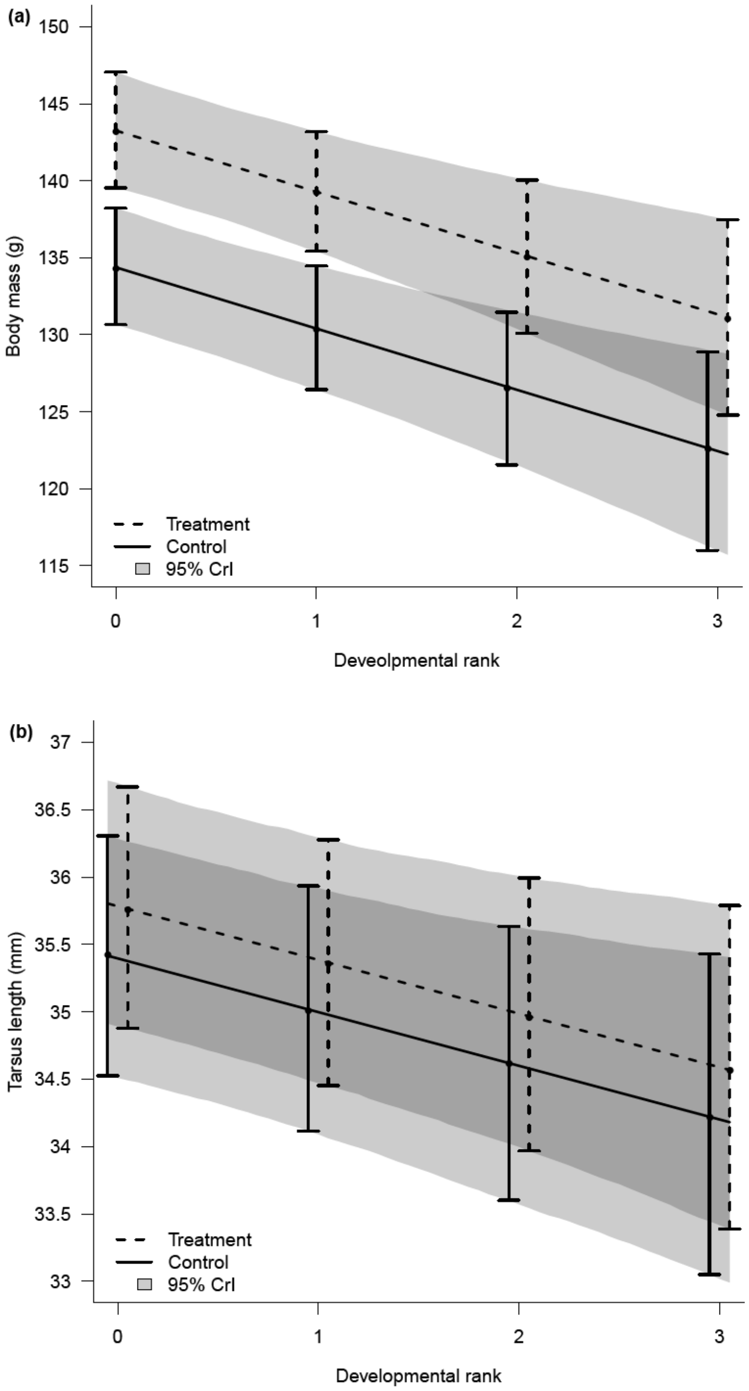

Fig. 3. Effect of developmental rank and experimental treatment on nestling (a) body mass, (b) tarsus length, (c) survival probability and (d) the probability of struggling when handled. A developmental rank of zero represents the first-hatched little owl within a family. The shown effects were predicted for 30-day-old nestlings. The dashed and solid lines represent the food-supplemented and control group, respectively. Ninety-five per cent CrI from the posterior distribution are shaded in grey. Sample sizes are given in Table 2.

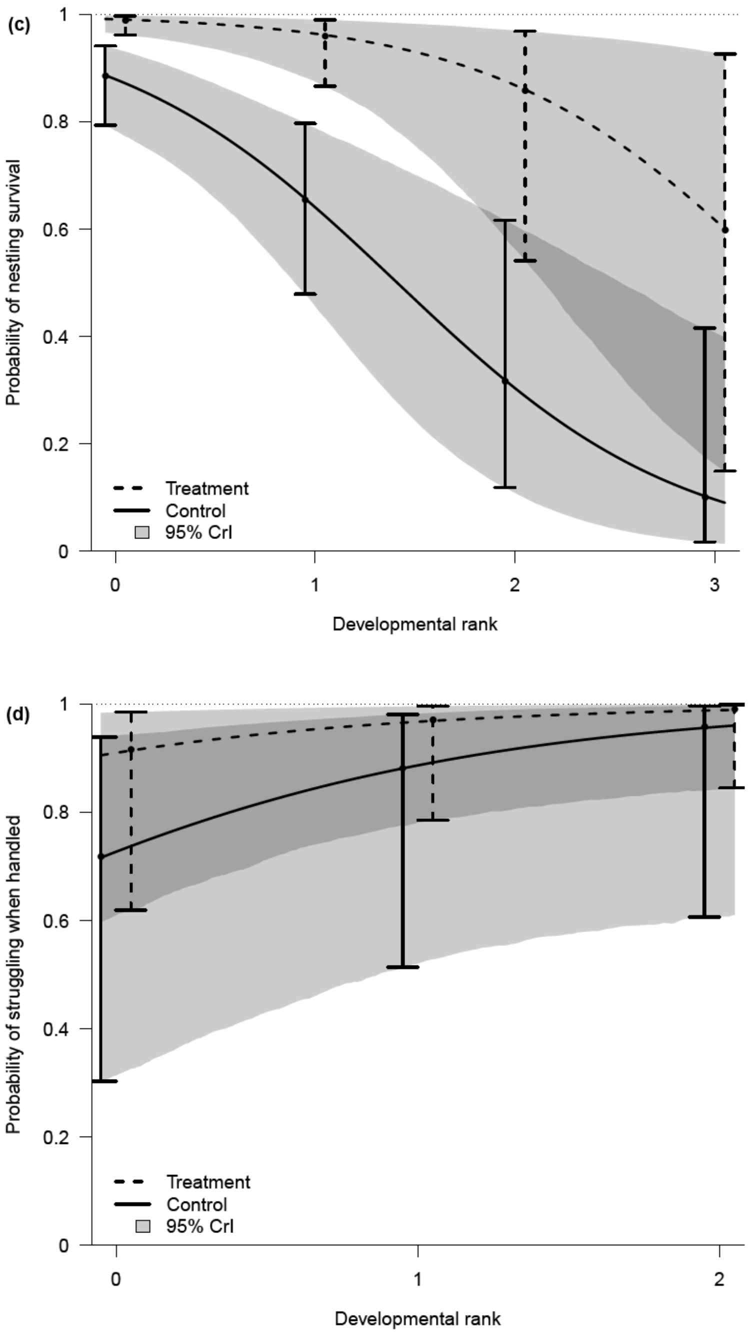

Fig. 3. (*continued*)

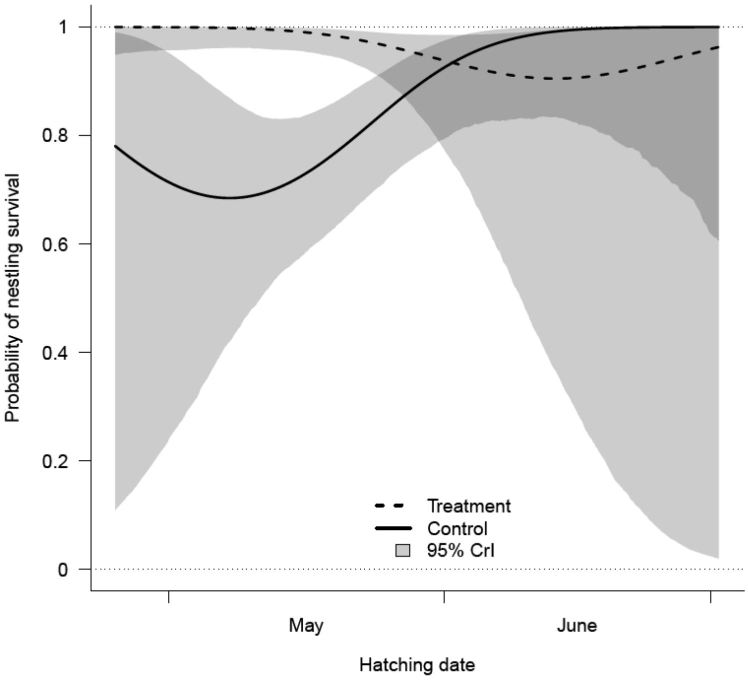

Fig. 4. Effects of hatching date and experimental treatment on little owl nestling survival. The dashed and solid lines represent the food-supplemented and control group, respectively. The 95% CrI from the posterior distribution is shaded in grey. Sample sizes are given in Table 2.

CHAPTER 2

Variation in energy supply drives post-fledging survival and reproductive output in little owls (*Athene noctua*)

Marco Perrig, Martin U. Grüebler, Herbert Keil & Beat Naef-Daenzer

To be submitted

Abstract

The early post-fledging stage is a major bottleneck of survival in altricial birds and has profound consequences on reproductive success. Amongst the range of factors potentially influencing post-fledging survival, the energy flow to juveniles likely plays a central role. However, the exact mechanism shaping post-fledging survival is little understood. Conducting a food supplementation experiment we determined the effect of food supply on survival patterns of juvenile little owls (*Athene noctua*) from hatching to two months post-fledging. Experimental broods were supplemented during 36 days during the nestling and the early post-fledging period. The fate of 307 juveniles (95 of them provided with extra food) was determined by nest controls and radio-telemetry. Overall, experimental food supplementation increased survival over the first three months of life from 47.2% to 62.1%. In supplemented birds, fortnightly survival rates were lowest during the nestling stage and steadily increased after fledging. Food supplementation substantially increased nestling survival, but had no direct effect on post-fledging survival. However, food supplementation indirectly affected the post-fledging stage. Heavy fledglings and fledglings with fat deposits were c. 50% more likely to survive the post-fledging period than light fledglings and fledglings with no fat deposits. This suggests that energy carried over from the nestling stage is a major determinant of post-fledging survival. The low nestling and post-fledging survival shows that the early life-history stages constitute a crucial bottleneck of reproductive ecology in little owls. The strong direct and indirect effects of food supplementation on nestling and post-fledging survival, respectively, revealed that variation in food supply is an important determinant of this life-history bottleneck. The effect of energy supply was particularly strong during the nestling stage when energetic requirements and sibling competition are high. Energy reserves accumulated during the nestling stage likely facilitate the development of essential skills such as foraging in the post-fledging period.

Keywords

Post-fledging survival, trophic relationship, food supplementation, radio-telemetry.

Introduction

Juvenile survival is generally lower than adult survival and plays an important part in population dynamics (e.g. Crouse *et al.* 1987; Gaillard *et al.* 2000). In altricial birds, the early post-fledging stage is a major bottleneck (e.g. Grüebler *et al.* 2014; reviews in Maness & Anderson 2013; Cox *et al.* 2014). Survival over the first three weeks after fledging can be as low as 23% in passerine birds (Cox *et al.* 2014). Thus, post-fledging survival has the potential to substantially affect reproductive success by limiting the number of offspring which survive to their first breeding season. This makes post-fledging survival an essential component of reproductive ecology, with ultimate consequences for individual fitness and population dynamics (Todd *et al.* 2003; Cox *et al.* 2014).

A multitude of factors potentially shape post-fledging survival, including species-specific traits (e.g. hatching synchrony), parental characteristics (e.g. foraging performance, brood size, timing of breeding), juvenile traits (e.g. sex, fledgling phenotype, individual personality), and environmental conditions (e.g. food resources, weather; Sih *et al.* 2004; Maness & Anderson 2013; Cox *et al.* 2014). Most of these factors at least partially link to the trophic chain – food supply in particular. For example, food availability influences clutch size and hatching date (e.g. Martin 1987; Nager *et al.* 1997; van Nieuwenhuyse *et al.* 2008). Mediated through parental performance, food availability also affects phenotypic development of chicks (Simons & Martin 1990; Dewey & Kennedy 2001; Granbom & Smith 2006; Wellicome *et al.* 2013). In turn, fledgling phenotypic traits affect post-fledging survival (e.g. Naef-Daenzer *et al.* 2001; Grüebler & Naef-Daenzer 2010). Thus, besides direct effects (i.e. growth rates, starvation), variation in food supply may also carry over from the nestling stage into later life-history stages and indirectly affect post-fledging survival via physical traits or behavioural performance. Therefore, we believe that food availability plays a central role in shaping post-fledging survival patterns and thus, in driving evolutionary adaptations of reproductive traits to environmental conditions. However, the exact mechanism how the energy flow to juveniles influences post-fledging survival patterns is poorly understood. Experimental evidence for the post-fledging stage is largely missing, especially for non-passerine birds.

Nestling food supply affects fledgling quality, including for example behavioural traits, structural size and energy reserves (e.g. Martin 1987; Boutin 1990; Dewey & Kennedy 2001; Perrig *et al.* 2014). These traits persist beyond fledging and may affect post-fledging survival and future reproductive success. In combination with post-fledging food supply, individual quality affects the energetic state of post-fledging juveniles. Energetically limited individuals may starve. They may also be more vulnerable to predation because they are worse in evading predators (Veasey *et al.* 2000; Jones *et al.* 2009), because they spend more time foraging (e.g. MacLeod *et al.* 2005) or because they beg more often and more intensively (Berthold 1976) than energetically less limited individuals. Furthermore, energetically limited individuals may be poor in coping with diseases compared to well-fed birds (Acquarone *et al.* 2002). Other individual traits (e.g. behavioural disposition, structural size) may accentuate or mitigate these risks.

The aims of this study were threefold. First, we investigated the temporal pattern of post-fledging survival in little owls (*Athene noctua*), expecting juvenile mortality to peak shortly after fledging (e.g. Low & Pärt 2009). Second, we determined the effects of variation in food supply on post-fledging survival using a food supplementation experiment. We hypothesize that experimental food supplementation improves post-fledging survival, but expect that this effect decreases with time as juveniles gradually learn to provide for themselves and to cope with potential hazards. Third, built on prior knowledge of the effects of nestling food supply on the phenotypic development of little owls (Perrig *et al.* 2014), we explored the carry-over effects from alimentary conditions during the nestling stage into the post-fledging stage and the effects of hatching date on juvenile survival. The experiment reveals the role of food limitation in driving post-fledging mortality in a small predatory bird and enhances our understanding of the underlying mechanism.

Materials and methods

This study was conducted in a population of about 220 little owl breeding pairs in Southern Germany (Landkreis Ludwigsburg, Baden-Württemberg, 48°53’43″N, 9°11’45″E). Virtually all pairs of this population breed in artificial nestboxes. From 2009 to 2011, 307 hatchlings in 93 broods were monitored from hatching to the onset of dispersal.

FOOD SUPPLEMENTATION

In 2010 and 2011, 14 pairs of synchronous broods were denoted as partner broods. One of them was randomly assigned to experimental treatment (i.e. food supplementation). Depending on brood size, one or two nestlings of similar age and body mass were exchanged among partner broods, keeping brood sizes constant (for details see Perrig *et al.* 2014). An additional 13 broods in 2009, 4 broods in 2010 and 20 broods in 2011 were included in the analysis. No cross-fostering was conducted in these additional broods, but in 2011, three of them were also food supplemented. Food supplementation started when the nestlings were c. 14 days old. After treatment start, all 93 broods were visited every other day for 36 days. During these visits a total of 480 g of dead laboratory mice per nestling was deposited inside the nestbox of supplemented broods, 20 g per visit and nestling for the first six visits, 30 g per visit and nestling thereafter. Thus, control broods and experimental broods were treated equally (i.e. regularly visited) except that no food was supplied to control broods. Mice were chosen as supplementary food because rodents are the major component of nestling food supply in little owls (van Nieuwenhuyse *et al.* 2008; Müller 2012). Food supplementation represented a c. 40% increase compared to natural food supply (Juillard 1984). Visits (and food supplementation) continued beyond fledging (at c. 30 days of age, when nestlings leave the nestbox for the first time). After little owl nestlings leave their nestbox for the first time, their flight capacity is still limited. They stay within close proximity of the nestbox and regularly return for food and shelter. For this study, we defined the post-fledging stage as the time from fledging to the onset of dispersal at c. three months of age.

MONITORING SURVIVAL

The survival of individuals was determined using nest controls, camera traps and radio-telemetry. Nestboxes were checked every two to three days during the entire nesting period. In addition, camera traps (Reconyx Hyperfire HC500, Wisconsin, USA) were installed to monitor the entrance of all nestboxes in 2011 during the period of food supplementation. At the age of 28.7 days ± 2.93 (mean ± 1 SD, $n = 239$) all surviving nestlings were tagged with VHF radio-transmitters of own construction (Naef-Daenzer *et al.* 2005). The tags were mounted with a back-pack figure-8-harness (Kenward 2001). Life expectancy of the tags was c. 400 days and the range with handheld 3-element Yagi antennas was up to 40 km. The total tag weight (including harness) was c. 7 g. This is 4.5% of the mean body mass of adults captured during our study (i.e. less than the maximum of 5% generally recommended; Caccamise & Hedin 1985; Kenward 2001; Jackson *et al.* 2011). After tagging, all individuals were located at least three times per week to check whether they were alive or not. If possible, the cause of death was determined.

ANALYSES

Nestling and post-fledging survival was analysed using Cormack–Jolly–Seber (CJS) mark–recapture models (Lebreton *et al.* 1992) in the software MARK 6.1 (White & Burnham 1999). All live encounters after hatching were used to build re-encounter histories for seven fortnightly intervals. Thus, the data encompassed the first 3 months after hatching. The first two survival estimates refer to nestling survival (i.e. survival to day 28 post-hatching). The remaining four survival rates represent post-fledging survival to day 84 post-hatching (i.e. to the onset of dispersal).

Nestling survival Φ_{Nest} and post-fledging survival Φ_{Post} (i.e. survival after leaving the nestbox) are most likely governed by a different set of factors (Dybala *et al.* 2013). Therefore, we modelled separate effects for Φ_{Nest} and Φ_{Post}. The maximal model included age-dependent survival rates with an additive year effect for both, Φ_{Nest} and Φ_{Post}. To test for differential effects of experimental food supplementation on Φ_{Nest} and Φ_{Post}, a separate treatment effect was included. To estimate temporal variation in the treatment effect, an interaction between time and treatment was added for Φ_{Post}. Factors inherent to family units (e.g. genetic factors, common nest environment) can cause interdependence of survival rates among family members. Randomisation of the treatment and partial cross-fostering prior to experimental food supplementation partially controlled for such effects. To control for potential effects of the exchange itself, an additive exchange effect was added for exchanged individuals. The re-encounter probability p was allowed to vary with age and between years.

Model selection

Model selection was based on the Akaike Information Criterion adjusted for small sample size and overdispersion ($\mathrm{QAIC_c}$, Burnham & Anderson 2002). Parametric bootstrapping was run for 1000 simulations to assess the goodness-of-fit (GOF) of the maximal model $\Phi_{\mathrm{Nest\ (age\ +\ treatment\ +\ year\ +\ exchange)}}$ $\Phi_{\mathrm{Post\ (age\ +\ treatment\ +\ year\ +\ exchange\ +\ age\ \times\ treatment)}}$ $p_{\mathrm{(age\ +\ year)}}$. The resulting overdispersion parameter $\hat{c}_{\mathrm{bootstrap}}$ was 1.623. This was preferred over the medium-ĉ approach resulting in a less conservative estimate of the overdispersion parameter ($\hat{c}_{\mathrm{median}} = 1.429$).

Model selection from sets of *a priori* defined models was conducted in two steps. First, keeping Φ as in the maximal model, the best model for p was selected among four models: constant and age-dependent p with and without an additive year effect. Re-encounter rates were best modelled as constant without any year effect (i.e. $p_{(.)}$). Second, using $p_{(.)}$ to model re-encounter rates, model selection was conducted for Φ.

We assessed four factors potentially affecting Φ_{Nest} and Φ_{Post}: (i) constant or age-dependent, (ii) with or without a treatment effect, (iii) year dependent or not, and (iv) affected by the exchange or not. Because we expected a treatment effect during the post-fledging stage to diminish with time, the interaction between age and treatment for Φ_{Post} was also considered. The candidate model set included all possible models for Φ_{Nest} while keeping Φ_{Post} maximal and *vice versa* (i.e. a total of 35 models). Model selection within one part of a model will depend on the parameterization of the remaining part of the model (e.g. Burnham & Anderson 2002; Crawley 2005). To partially control for this, the candidate model set further included all possible models for Φ_{Nest} while using the best model for Φ_{Post} and *vice versa*. Within the resulting 68 models, Φ_{Nest} was selected among models with the best as well as the maximal model for Φ_{Post}, and *vice versa*.

Carry-over effects from the nestling stage

Nestling food supply affects a range of phenotypic traits in little owl fledglings. Body mass, wing length, the presence of subcutaneous fat deposits under the wing, and the probability of struggling when handled were all positively affected by experimental food supplementation (Perrig *et al.* 2014). Furthermore, food supplementation reduced tonic immobility time and the intensity of eye coloration (Perrig *et al.* 2014). These traits represent different potential mechanisms linking nestling food supply to post-fledging survival. For example, wing length is closely related with flight capacity (Pennycuick 2008), fat deposits represent energy stores (Jenni & Jenni-Eiermann 1998) and eye coloration is linked to nutritional quality (Oliphant 1987; Hill & McGraw 2006) and may have a function in intraspecific interactions (Newton & Marquiss 1982; Bortolotti *et al.* 2003; Guillemain *et al.* 2012). In a first step, we determined which of these six traits correlated with post-fledging survival. Based on the best model resulting from the model selection for Φ described above (hereafter called baseline model), we compared models with and without traits added as individual covariates to Φ_{Post}. Traits improving the baseline model for Φ_{Post} by two $\mathrm{QAIC_c}$ units or more were considered to correlate with post-fledging survival (Burnham & Anderson 2002; Arnold 2010). In a second step, all additive combinations of influential traits identified in step 1 where then modelled to jointly determine their relative contribution in explaining variation in post-fledging survival. In addition, we tested in a third step if separate correlations between post-fledging survival and the same influential traits existed for the treatment and control group alone.

Individual attributes were measured several times during the nestling stage (for details see Perrig *et al.* 2014). Here, we used the measurements closest to fledging. Because morphological measures (i.e. body mass and wing length) are age dependent, the residuals of measurements on the fitted growth curves through all data points (TableCurve 2D Version 5.01, Systat Software Inc., Erkrath, Germany) were used for the analysis. In 2009, only body mass was measured. Thus, the remaining five traits were only included as covariates for 2010 and 2011. Mean substitution within groups was used to substitute missing data.

Effects of the timing of breeding

In a post-hoc test, the effect of timing of breeding (i.e. hatching date) on juvenile survival was estimated based on the baseline model. Experimental food supplementation may affect a potential hatching date effect because the effect is likely linked to natural food availability (van Noordwijk *et al.* 1995). Furthermore, the potential effect may depend on the life-history stage (Dybala *et al.* 2013). Thus, separate hatching date effects for Φ_{Nest} and Φ_{Post} within the treatment and control group were added as individual covariates to the baseline model.

Results

MODEL SELECTION

The best model for fortnightly survival rates (Φ) included a constant treatment effect during the nestling stage and an age effect during the post-fledging stage ($\Phi_{\text{Nest (treatment)}}$ $\Phi_{\text{Post (age)}}$; Table 1). Neither partial cross-fostering nor the year had any effect on nestling or post-fledging survival.

CHARACTERISTICS OF SURVIVAL

For the control group, fortnightly survival rates of juvenile little owls were lowest during the nestling stage ($\Phi_{\text{Nest-Control}}$ = 0.822 ± 0.026; estimate ± SE; Fig. 1). Thus, 67.5 ± 4.2 % (estimate ± SE) of control hatchlings survived this stage. After fledging, survival rates increased steadily with age to reach 0.965 ± 0.019 (estimate ± SE) at three months post-hatching. At this time, juvenile survival rates approached mean fortnightly survival rates of adult little owls across the year (own unpubl. data). Overall, 47.2 ± 3.9 % (estimate ± SE) of all control hatchlings survived the first three months.

Predation was the main cause of mortality during the post-fledging period. 81.8% of all determined casualties (*n* = 55) were caused by avian or mammalian predation.

EFFECTS OF FOOD SUPPLEMENTATION

Experimental food supplementation substantially increased nestling survival rates ($\Phi_{\text{Nest-Treatment}}$ = 0.942 ± 0.021; estimate ± SE; Fig. 1). 88.8 ± 3.9 % (estimate ± SE) of all supplemented hatchlings survived till fledging. In contrast, models including an experimental effect after fledging received little support (Table 1). According to the favoured model, fortnightly survival rates dropped to control levels (Fig. 1), rising with age thereafter. Thus, experimental treatment had a marked effect on nestling, but not on post-fledging survival. Overall, 62.1 ± 4.4 % (estimate ± SE) of all supplemented hatchlings survived the first three months.

CARRY-OVER EFFECTS FROM THE NESTLING STAGE

Although unaffected by experimental food supplementation, post-fledging survival varied with other factors under consideration. Post-fledging survival rates were positively correlated with body mass ($\Delta QAIC_c$ = -3.03) and the presence of fat deposits ($\Delta QAIC_c$ = -3.93) at fledging (a $\Delta QAIC_c \leq -2.0$ is considered relevant; Table 2). Within the control group, estimates of fortnightly survival rates of fledglings without subcutaneous fat deposits dropped below estimates of nestling survival, but rose thereafter (Fig. 2a). In contrast, survival rates of control fledglings with fat deposits continuously improved from fledging onwards (Fig. 2a). In total, the presence of fat deposits at fledging increased post-fledging survival by almost 50%. Cumulative post-fledging survival was 75.5 ± 4.2% (estimate ± SE) for fledglings with fat deposits compared to 52.8 ± 3.3% (estimate ± SE) for fledglings without fat deposits (Fig. 2b). The positive effect of residual fledgling body mass showed a similar pattern (Fig. 2c). Heavy fledglings had higher survival rates during the post-fledging stage than light fledglings. Thus, observed survival was strongly dependent on body condition, selecting for heavy individuals with fat deposits. As a result of differential survival, the population means (in terms of residual body mass and fat deposits) increased with age (Fig. 3).

The model including both fledgling body mass and fat deposits was not better supported than models including only one of these factors (Table 2). The effect of body mass and presence of fat deposits on post-fledging survival was also found within the control group alone, but not within the food supplemented group alone (Table 2). We did not detect effects of other phenotypic traits affected by nestling food supply (i.e. wing length, countenance when handled, tonic immobility and eye coloration) on post-fledging survival. Thus, post-fledging survival appeared to be indirectly affected by nestling food supply via the effects on body mass and/or accumulated fat reserves.

EFFECTS OF THE TIMING OF BREEDING

Including an effect of timing of breeding (i.e. the hatching date) improved model fit considerably ($\Delta QAIC_c = -4.05$). Hatching date had a pronounced effect on nestling survival ($\beta_{Nest\text{-}control} = 0.046$, 95% CI = 0.001 – 0.089; $\beta_{Nest\text{-}treatment} = -0.100$, 95% CI = -0.174 – -0.027) but not on post-fledging survival ($\beta_{Post\text{-}control} = 0.009$, 95% CI = -0.026 – 0.044; $\beta_{Post\text{-}treatment} = 0.000$, 95% CI = -0.045 – 0.045). Thus, control chicks hatched at the end of May were more likely to survive the nestling period than chicks hatched at the beginning of May. In contrast, the reverse pattern was detected for experimentally supplemented chicks.

Discussion

SURVIVAL PATTERNS

Survival of unsupplemented young little owls was lowest during the nestling stage and steadily increased after fledging. Thus, the nestling stage contributed considerably towards the bottleneck of juvenile survival. This pattern contrasts with patterns reported for passerine birds where survival rates drop sharply upon fledging (e.g. Keedwell 2003; Sunde 2005; review in Cox *et al.* 2014). It is probably related to different reproductive strategies of owls and passerines. Asynchronous hatching is common in owls (Collingwood 1959) and favours sibling competition and aggression, potentially leading to brood reduction (Mock *et al.* 1990; Stenning 1996). In periods of food shortage, older siblings may monopolize the access to delivered food items due to their physical superiority, leading to the starvation of younger siblings (Forbes & Mock 2000; Drummond 2001). Thus, variation in nestling food supply to little owls results in improved survival rates of youngest siblings (Perrig *et al.* 2014).

THE ROLE OF FOOD SUPPLY

Our experiment clarified that food supply during growth is an important driver of little owl survival from hatching to dispersal. For food supplemented hatchlings, the chances to survive to fledging were almost one third higher than for control hatchlings. This was probably due to a reduction in sibling competition (see discussion above). While the experimental treatment did not directly improve post-fledging survival, it had marked indirect effects. Post-fledging survival correlated with individual traits that were themselves affected by experimental food supplementation. For example, the presence of subcutaneous fat deposits at fledging depended on nestling food supply (Perrig *et al.* 2014). In turn, fat deposits at fledging increased the chances to survive the post-fledging stage by more than 40%, regardless of experimental treatment. Thus, food supply during growth is probably the key determinant of both, nestling and post-fledging survival. Since juvenile survival is an important predictor of life-time reproductive success (Newton 1989), nestling food supply ultimately affects reproductive success and population dynamics.

Among the variables known to be affected by nestling food supply (Perrig *et al.* 2014), only fledgling body mass and the presence of fat deposits affected post-fledging survival. While body mass is a compound trait that may represent a variety of factors (e.g. energy stores, muscle mass, size; Schulte-Hostedde *et al.* 2005; Labocha & Hayes 2012), the presence of fat deposits specifically represents energy reserves (Jenni & Jenni-Eiermann 1998). Since adding body mass to a model including fat deposits did not improve model fit, we conclude that energy reserves acquired during the growth period are the main factor affecting post-fledging survival.

Although predation was the major proximate cause of death during the post-fledging stage, energetic constraints may be an important underlying factor. Individuals of good physical condition may beg less frequently and less vigorously (Berthold 1976), may spend more time being vigilant (Jones *et al.* 2009) and may be superior in escaping predation than underfed individuals (Veasey *et al.* 2000). Thus, physical condition may affect both an individual's exposure to risk and its response to potential attacks. Further evidence is required to determine the exact mechanism behind post-fledging mortality.

In contrast to the marked effect of food supplementation during the nestling period we did not detect a direct treatment effect on post-fledging survival. We consider two explanations for this result. First, physical development (and the associated high energy demand) is largely completed after fledging (Martin 1987) and thus, constraints in food supply may be reduced. In addition, chicks start providing for themselves after fledging and rely less on parental food supply than during the nestling stage. Thus, the magnitude of a potential experimental effect during the post-fledging period is probably substantially smaller compared to the nestling period. Moreover, the good physical condition of food supplemented little owl fledglings (Perrig *et al.* 2014) probably further reduced constrains in post-fledging food supply and thus, a potential experimental effect. This is supported by the finding that survival rates correlated with fat deposits and body mass for the control group alone, but not for the treatment group alone. Second, a direct treatment effect during the post-fledging period is likely confounded by numerous factors acting outside the nestbox. Not all chicks may continue to access the supplemented food. Also, between-territory variation in food availability, predation pressure, availability of cavities and other external factors may add additional variance to survival rates that conceals the potential effect of food supplementation.

CONSEQUENCES FOR REPRODUCTIVE ECOLOGY

Overall, supplemented broods produced considerably more independent young than control broods. This effect of food supplementation suggests that reproductive success improves with increasing natural food availability. Indeed, we found that nestlings from control broods survived better if they hatched later in the breeding season (this study) when rodents became more abundant (own unpubl. data). Experimental food supplementation compensated for this natural variation in food availability. We conclude that the survival of juvenile little owls (and in turn the ultimate reproductive output) may greatly vary in relation to spatial and temporal variation in food resources. In order to maximize their reproductive output, parents are thus expected to adjust the hatching date of their clutch to match peaks in natural food availability (Naef-Daenzer & Keller 1999; but see Drent 2006).

The food-driven selective survival of juvenile little owls indicates a potential for evolutionary feedback mechanisms shaping reproductive traits in response to environmental factors. Natural food availability and accessibility as well as parental decisions and performance determine the energy flow to juveniles (van Noordwijk *et al.* 1995; Grüebler & Naef-Daenzer 2008; Eldegard & Sonerud 2010). In turn, differential juvenile mortality may result in the selection of (heritable) reproductive characteristics.

In conclusion, this study highlights the trophic chain as a fundamental driver of juvenile survival patterns. It contributes to clarifying the link between environmental conditions in terms of food availability, variation in reproductive success and key demographic parameters. Local variation in the number of juveniles surviving the post-fledging stage in relation to the energetic conditions during the growth period limits the number of potential recruits into the breeding population. Furthermore, the number of post-fledging birds dispersing into surrounding populations is important for meta-population dynamics. Immigrants have been shown to be the major determinant of sub-population persistence of little owls (Schaub *et al.* 2006). Thus, food supply during growth not only shapes survival patterns during a bottleneck in the life-history of little owls, but also determines higher-level dynamic processes such as fecundity, recruitment rates and the intensity of exchange of individuals among sub-populations.

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Table 1. Results of the five best models of model selection among the 68 candidate models separately modelling nestling (Φ_{Nest}) and post-fledging survival (Φ_{Post}) while keeping re-encounter rates constant. The best model for survival included a treatment effect (i.e. experimental food supplementation) for Φ_{Nest} while Φ_{Post} depended solely on age. Results are adjusted for small sample size and overdispersion ($\hat{c}$ = 1.623). $\Delta QAIC_c$ is the difference in $QAIC_c$ in reference to the best model.

Model	$QAIC_c$	$\Delta QAIC_c$	Num. Par.	QDeviance
$\Phi_{Nest\ (treatment)}\ \Phi_{Post\ (age)}$	569.4130	0	7	555.3277
$\Phi_{Nest\ (treatment\ +\ exchange)}\ \Phi_{Post\ (age)}$	571.0518	1.6388	8	554.9421
$\Phi_{Nest\ (treatment)}\ \Phi_{Post\ (age\ +\ treatment)}$	571.3360	1.9230	8	555.2262
$\Phi_{Nest\ (treatment)}\ \Phi_{Post\ (age\ +\ exchange)}$	571.3442	1.9312	8	555.2345
$\Phi_{Nest\ (age\ +\ treatment)}\ \Phi_{Post\ (age)}$	571.4337	2.0207	8	555.3239

Table 2. Results of the models used to test the influence of individual covariates on post-fledging survival (Φ_{Post}). Nestling survival was modelled as a function of experimental treatment and re-encounter rates were kept constant. Models including body mass or fat deposits as an individual covariate were better supported than the model without individual covariates. Model fit was also improved if these covariates were included for the control group alone, but not if included for the treatment group alone. Adding both covariates (i.e. body mass and fat) did not improve the models including just one of them. Results are adjusted for small sample size and overdispersion ($\hat{c}$ = 1.623). $\Delta QAIC_c$ is the difference in $QAIC_c$ in reference to the model with no individual covariate included ($QAIC_c \leq -2.0$ is considered relevant).

Model	$QAIC_c$	$\Delta QAIC_c$	Num. Par.	QDeviance
Φ_{Post} (age + body mass-control)	565.0423	-4.3707	8	548.9325
Φ_{Post} (age + fat)	565.4431	-3.9699	8	549.3333
Φ_{Post} (age + body mass + fat)	565.5083	-3.9047	9	547.3710
Φ_{Post} (age + body mass)	566.3791	-3.0339	8	550.2693
Φ_{Post} (age + fat-control)	566.5782	-2.8348	8	550.4685
Φ_{Post} (age + struggling)	568.8908	-0.5222	8	552.7811
Φ_{Post} (age)	569.4130	0	7	555.3277
Φ_{Post} (age + TI time)	570.5348	1.1218	8	554.4250
Φ_{Post} (age + wing)	570.6010	1.1880	8	554.4913
Φ_{Post} (age + eye colour)	571.2330	1.8200	8	555.1233
Φ_{Post} (age + body mass-treatment)	571.3600	1.9470	8	555.2502
Φ_{Post} (age + fat-treatment)	571.4263	2.0133	8	555.3165

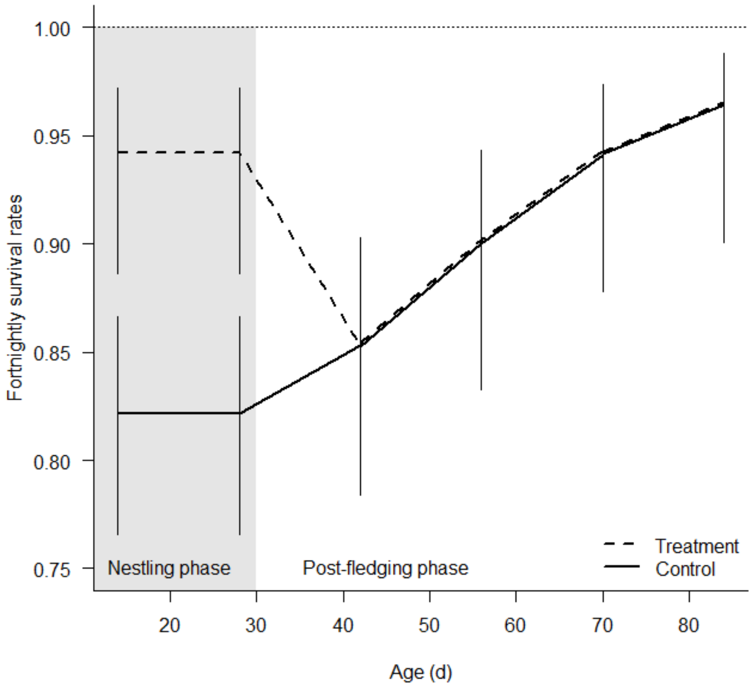

Fig. 1. Fortnightly survival rates of the food supplemented (dashed line, *n* = 105) and control (solid line, *n* = 202) group from the model $\Phi_{\text{Nest (treatment)}}\ \Phi_{\text{Post (age)}}\ p_{(.)}$. Vertical bars represent the 95% CI. The grey and white areas represent the nestling and post-fledging stage, respectively. Experimental food supplementation had a marked effect during the nestling stage, but not during the post-fledging stage.

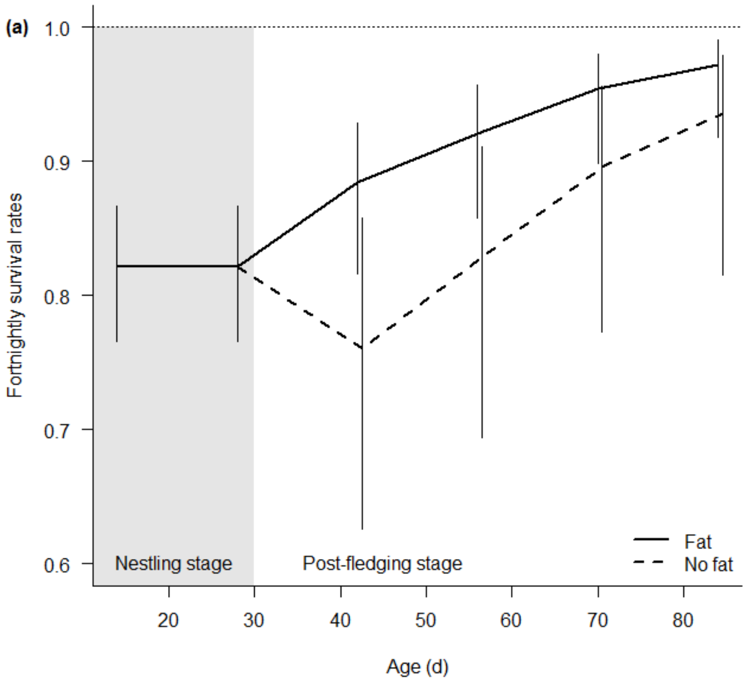

Fig. 2. (a) Fortnightly survival rates for fledglings of the control group with (solid line) and without (dashed line) fat deposits from model $\Phi_{\text{Nest (treatment)}}\ \Phi_{\text{Post (age + fat)}}\ p_{(.)}$. (b) Cumulative survival from the same model for fledglings with (black) and without (grey) fat deposits for both, the treatment (dashed line) and the control (solid line) group. (c) Fortnightly survival rates from model $\Phi_{\text{Nest (treatment)}}\ \Phi_{\text{Post (age + body mass)}}\ p_{(.)}$ for individuals of the control group with different fledgling body mass (colour from black to light grey represent the 97.5, 75, 50, 25 and 2.5 quantiles of the body mass distribution of fledglings, respectively). Vertical bars represent the 95% CI. The grey and white areas represent the nestling and post-fledging stage, respectively. The analysis was based on 307 hatchlings in three years. The 95% confidence intervals of cumulative survival were determined using the delta method (Powell 2007) and the beta distribution. Survival of individuals with fat deposits at fledging was markedly increased compared to individuals with no fat. Similarly, heavy individuals had better chances to survive the post-fledging stage than light individuals.

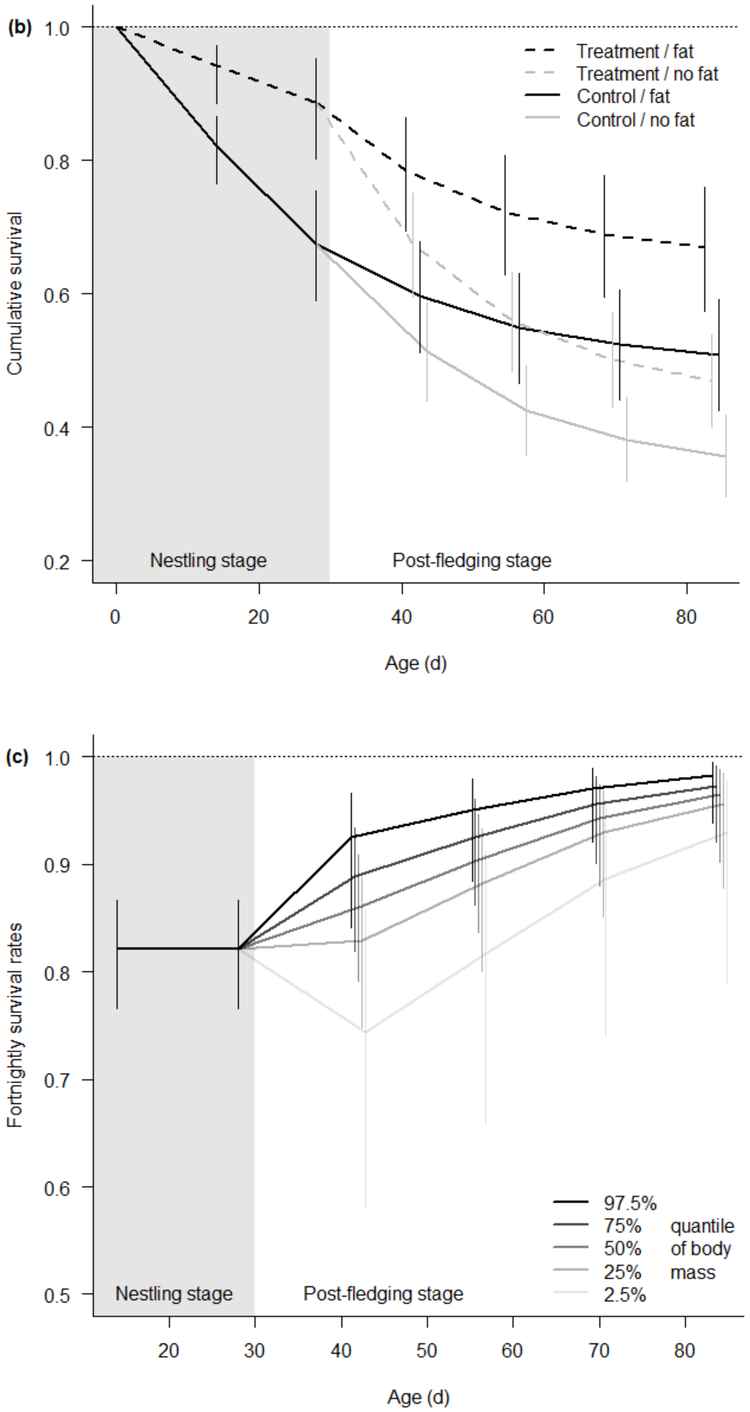

Fig. 2. (*continued*)

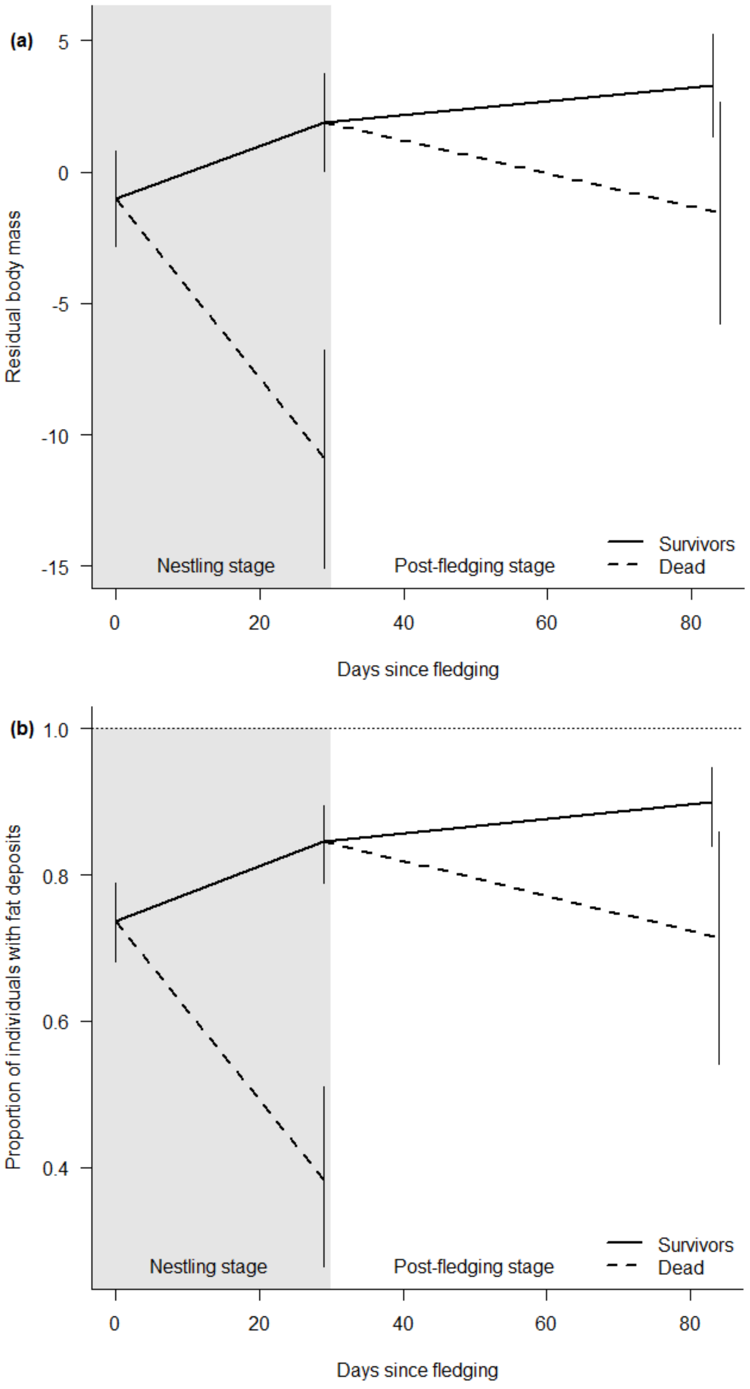

Fig. 3. Individual fledgling traits of juvenile little owls dying during (dashed line) and surviving (solid line) the nestling and the post-fledging stages. The traits represented here are (a) the residual body mass and (b) the proportion of individuals with fat deposits. Vertical lines represent the 95% CI. The clear discrepancy between traits of surviving and dead individuals indicates selective survival in favour of heavy individuals and for individuals with fat deposits.

CHAPTER 3

Is natal dispersal costly? Comparing survival rates across life-history stages from independence to first reproduction in little owls (*Athene noctua*)

Marco Perrig, Martin U. Grüebler, Herbert Keil & Beat Naef-Daenzer

To be submitted

Abstract

In altricial birds, juvenile survival is generally low compared to survival of later life-history stages. The proportion of juveniles surviving the first year of life varies largely in relation to parental breeding decisions, individual traits and environmental conditions. Thus, knowing the determinants of survival in the sequence of life-history stages from fledging to first reproduction is crucial to understand the mechanisms behind key demographic processes. However, few empirical studies investigated survival rates for all stages from fledging to first reproduction. Here we analyse survival of little owls (*Athene noctua*) from independence to first reproduction. We conducted a food supplementation experiment to assess the potential impact and carry-over effects of food supply during growth on later stages. Occasional periods of snow cover with sudden drops of food availability further allowed testing the impact of foraging conditions on survival during winter. Juvenile little owls (n = 167) were tracked for their entire first year of life using VHF radio-telemetry. Observations were aggregated into fortnightly encounter intervals, allowing survival estimates at a high temporal resolution. Survival was modelled in relation to life-history stages, experimental treatment and individual traits measured at fledging (i.e. body mass, the presence of fat deposits, tarsus length, wing length, countenance and eye coloration). First-year survival varied amongst the life-history stages. Estimated stage-specific survival was 0.706 for the dispersal stage, 0.963 for post-dispersal, 0.652 for winter, 0.882 for the incubation period and 0.728 when little owls reared their first brood. First-year survival also varied in response to environmental conditions. We found a strong effect of weather conditions on winter survival. However, we did not detect any significant carry-over effect of food supplementation during growth or of individual traits at fledging on survival rates from independence to first reproduction. Survival during the dispersal stage was reduced compared to later stages. However, the mortality observed during extended periods with snow cover exceeded the losses during dispersal. The finding that the experimental treatment did not carry over to later stages underlines that the effects of food supply on survival act on a short term rather than over longer periods. In conclusion, mortality rates were substantial during natal dispersal of little owls. However, the dispersal stage does not appear to be the only bottleneck during the first year of life. Limited food supply also caused high mortality in winter. Thus, natal dispersal and food supply are both important determinants of the proportion of juveniles surviving to first reproduction.

Keywords

Costs of dispersal, stage-specific juvenile survival, survival to first reproduction, carry-over effects, food supplementation, winter mortality.

Introduction

In altricial birds, survival of juveniles is known to be strongly reduced compared to adults (Clark & Martin 2007; Robinson *et al.* 2007; Tarof *et al.* 2011; Redmond & Murphy 2012). Thus, the juvenile stage is considered a major life-history bottleneck (review in Cox *et al.* 2014) and factors affecting juvenile survival will also affect recruitment rates and, ultimately, parental fitness and population dynamics (Newton 1989; Robinson *et al.* 2004; Clark & Martin 2007; Le Gouar *et al.* 2011). From hatching to first reproduction, individuals live through a sequence of ontogenetic stages. Survival rates in each stage are likely affected by different determinants such as parental breeding decisions, individual traits and environmental conditions (Dybala *et al.* 2013). To fully understand the mechanisms behind juvenile survival and the consequences for life-history ecology it is important to know stage-specific costs in terms of survival and their determinants (Dybala *et al.* 2013; Maness & Anderson 2013). However, the contributions of different juvenile life-history stages and different determinants towards overall juvenile survival have barely been quantified (e.g. Robinson *et al.* 2004; Low & Pärt 2009; Dybala *et al.* 2013).

Individual performance during a specific life-history stage may not only be directly affected by factors acting during that stage, but also indirectly by factors operating earlier in life (Bonte *et al.* 2012). Among these, food supply during growth is considered a key factor of physical development which may carry over into the post-fledging period and later life-history stages (Ims & Hjermann 2001; Benard & McCauley 2008). Nestling food supply is largely determined by natural food availability and parental performance (Eldegard & Sonerud 2010). There is good evidence that nestling food supply affects the development of young individuals (e.g. Martin 1987; Simons & Martin 1990; Granbom & Smith 2006; for little owls: Perrig *et al.* 2014) and that individual traits of fledglings affect survival and behavioural performance during the post-fledging stage (Naef-Daenzer *et al.* 2001; Kennedy & Ward 2003; Naef-Daenzer & Grüebler 2008; but see Dehnhard *et al.* 2014). However, evidence for carry-over effects of nestling food supply on later life-history stages (e.g. the dispersal stage) is still scarce and experimental tests of the magnitude and duration of such effects are virtually inexistent.

The first year of life of many altricial birds includes the nestling stage, the post-fledging dependency period, natal dispersal, the courtship period and first reproduction. There is ample evidence that survival during the post-fledging period is low (review in Cox *et al.* 2014). The stage of natal dispersal is considered another crucial stage during which individuals incur elevated costs (Clobert *et al.* 2001; Clobert *et al.* 2012; Hardouin *et al.* 2012). These costs may be of different nature, including reduced survival rates in a life-history context (Bonte *et* *al.* 2012). Survival rates during natal dispersal are hypothesized to depend on the distance and duration of dispersal and on environmental factors (e.g. variation in food availability, predator and conspecific densities; habitat matrix; Pasinelli *et al.* 2004; Yoder *et al.* 2004; Matthysen 2005; Bonte *et al.* 2012; Bock *et al.* 2013). The relative importance of these determinants may depend on individual traits (i.e. energy reserves, personality; Ims & Hjermann 2001; Bowler & Benton 2005; Cote *et al.* 2010). Due to the difficulty of tracking individuals from independence to first reproduction, few studies have quantified the costs of dispersal in terms of survival and potential carry-over effects from growth.

The aims of this study were twofold. First, we determined stage-specific survival rates from independence to first reproduction in little owls (*Athene noctua*). Hereby, we set the costs of dispersal (in terms of survival) in relation to the costs of other life-history stages throughout the first year of life, including those of the nestling and post-fledging stages (Chapter 2). We hypothesized that survival rates during natal dispersal are reduced compared to later life-history stages. Second, we investigated the effects of an important environmental factor, food supply, on first-year survival patterns. To test for carry-over effects of food supply during juvenile development on later life-history stages, a food supplementation experiment during the nestling and early post-fledging period was conducted. We expected food supplementation to improve survival rates after reaching independence. Short-term variation in food accessibility (e.g. due to snow cover) further allowed assessing the impact of sudden declines in food availability on survival during winter.

Materials and methods

STUDY SPECIES AND STUDY AREA

The little owl is a territorial species with obligate natal dispersal. Normally, little owls first reproduce at an age of one year. For this study, the time period from 1 August to 2 July the following year was analysed, encompassing the time from the individuals' first explorations beyond the natal home range (i.e. after reaching independence) well into their first reproduction. Within this timeframe, we considered five distinct stages (defined by date) that relate to little owl development and seasonal changes in the environment (Table 1): natal dispersal, post-dispersal, winter and two stages for the first reproduction (i.e. incubation and brood rearing). The dispersal stage (August to October) includes pre-dispersal excursions and is characterized by the exploration of unknown areas. Major dispersal movements are expected in September and October (van Nieuwenhuyse *et al.* 2008). During the post-dispersal stage (November), the main dispersal movements are completed (van Nieuwenhuyse *et al.* 2008). In winter (December to mid-March) challenging climatic conditions may occur. In this period, territories are established and pair-formation takes place. The incubation stage (mid-March to mid-May) encompasses the time from egg-laying to hatching and the stage of brood rearing (mid-May to June) corresponds to the period of nestling provisioning.

This study was conducted in a population of about 220 little owl breeding pairs in Southern Germany (Landkreis Ludwigsburg, Baden-Württemberg, 48°53’43″N, 9°11’45″E). Virtually all pairs of this population breed in nestboxes. From 2009 to 2011, 93 broods were monitored from late incubation onwards using regular brood controls, camera traps and radio-telemetry. At the onset of independence 167 juveniles from 73 broods were still alive and, thus, included in this study.

DATA COLLECTION

Radio-telemetry

Prior to fledging, all chicks were tagged with VHF radio-transmitters of own construction (Naef-Daenzer *et al.* 2005). Tags were mounted with a back-pack figure-8-harness (Kenward 2001). Life expectancy of the tags was c. 400 days and the range with handheld 3-element Yagi antennas was up to 40 km. The total tag weight (including harness) was c. 7 g. This is 4.5% of the mean body mass of adults captured during our study (i.e. less than the maximum of 5% recommended in Caccamise & Hedin 1985; Kenward 2001; Jackson *et al.* 2011). We located all individuals at least three times per week using the homing-in technique (Kenward 2001). This allowed to detect whether birds were alive or to determine the causes of mortality. During the main dispersal stage in September and October (van Nieuwenhuyse *et al.* 2008), tracking was intensified to 4-5 re-locations per week.

Food supplementation

To experimentally test whether the effects of nestling food supply carry over beyond the post-fledging dependency period, a food supplementation experiment was conducted during the nestling and early post-fledging period. Food supplementation started when the nestlings were c. 14 days old. Of the 73 broods, 13 and 12 broods in 2010 and 2011, respectively, were food supplemented over a time period of 36 days. A total of 480 g of dead laboratory mice per nestling was deposited inside the nestbox of supplemented broods, 20 g per visit and nestling for the first six visits, 30 g per visit and nestling thereafter. Thus, food supplementation continued until juveniles were c. 50 days old (i.e. three weeks after fledging). Control broods were treated equally (i.e. visited every other day) except that no food was supplied. Further details of the experimental protocol are given in Perrig *et al.* (2014).

Individual traits

During tagging (at an age of 28.7 days ± 2.93; mean ± 1 SD; $n = 239$), six individual traits were measured: body mass (to the nearest 0.1 g), the presence or absence of subcutaneous fat deposits under the wing, tarsus length (to the nearest 0.1 mm), wing length (to the nearest 0.5 mm), countenance (i.e. struggling during handling or not) and eye coloration (i.e. intense or pale). For details see Perrig *et al.* (2014). In addition, feather samples were obtained for genetic sex determination of the nestlings.

Morphological measures (i.e. body mass, wing length and tarsus length) were measured several times during the nestling stage (for details see Perrig *et al.* 2014). Here, we used the measurements closest to fledging. Because these morphological traits are age dependent, residuals of these measurements on the fitted growth curves through all data points (TableCurve 2D Version 5.01, Systat Software Inc., Erkrath, Germany) were used for the analysis. In 2009, only body mass and tarsus length were measured. Thus, the remaining four traits (i.e. wing length, fat deposits, countenance and eye coloration) were only included as covariates for 2010 and 2011. Mean substitution within groups was used for missing data.

Environmental variables

To estimate food availability in winter, a winter rodent index was determined using life-trapping sessions in winter and early spring. In each session, 100 baited traps (Field Trip Trap Live Catch Trap, Alana Ecology, Bishops Castle, UK) were set for 72 h. They were placed at two sites within the study area, both frequented by little owls. Within site, five blocks of 10 traps were set at distances between 300 and 900 m. The same trapping locations were used for all sessions. Traps were checked and reset every 12 h. One trapping session in winter and one in early spring were conducted to determine the rodent index for the winter stages 2010/11 and 2011/12. For the rodent index of the winter stage 2009/10 only the early spring session was available. The rodent index used in the survival analysis represented the number of traps catching rodents averaged across trapping session within a particular winter.

In order to correlate survival rates with weather conditions in the area, three weather variables were calculated for each fortnightly interval using the daily weather data from the meteorological station Stuttgart-Echterdingen (Germany, station ID: 4931): mean temperature (°C), total precipitation (mm) and the number of days with a snow cover exceeding 3 cm.

ANALYSIS

Radio-tracking data were summarized into live encounter histories of 24 fortnightly intervals (i.e. 23 survival estimates). Survival rates were analysed using Cormack–Jolly–Seber (CJS) mark–recapture models (Lebreton *et al.* 1992) in the software MARK 6.1 (White & Burnham 1999).

Model selection

Model selection within sets of *a priori* defined models (see below) was based on the Akaike Information Criterion adjusted for small sample size and overdispersion ($QAIC_c$, Burnham & Anderson 2002). The median-ĉ approach (22 ĉ values between one and two, 100 simulations per ĉ) was used to assess the goodness-of-fit (GOF) of the maximal model without covariates: $\Phi_{(\text{time + year + treatment + sex + time x year + time x treatment})}\ p_{(\text{year + effort})}$. The resulting overdispersion parameter $\hat{c}_{\text{median}}$ was 1.872. This was preferred over the bootstrapping approach resulting in a less conservative estimate of the overdispersion parameter ($\hat{c}_{\text{bootstrap}} = 1.321$).

Temporal pattern of survival

To explore the temporal survival patterns, model selection was conducted in four steps. The first step selected the best re-encounter model *p*. Step two selected between fully time-dependent, stage-dependent and constant survival (Φ) models. Furthermore, it tested for effects of age and sex and an overall year effect on Φ. The subsequent two selection steps evaluated the resulting year effect of Φ in more detail. Step three identified stages contributing to the overall year effect and step four explored whether survival patterns in those stages related to environmental factors.

Starting model

The starting model for Φ was fully time-dependent. It included a year effect as well as the interaction time x year. The age of tagged individuals on 1 August varied considerably depending on the timing of breeding (29 – 87 days) and may have affected individual survival probabilities (Chapter 2). Thus, age (at 1 August) and the interaction time x age were included in the starting model. Furthermore, sex was also included. The model for the re-encounter probability *p* accounted for between-year variation and for varying sampling effort due to variations in manpower. Birds were not tracked during one interval in winter 2009/10 and three intervals in spring 2010. Re-encounter rates for these intervals were set to zero in all models. The resulting starting model was $\Phi_{(\text{time + year + age + sex + time x year + time x age})}\ p_{(\text{year + effort})}$.

Step 1: Re-encounter probability

Using the starting model for Φ, the best model for re-encounter probability *p* was selected among four models: constant or depending on effort, with and without an additive year effect. Re-encounter probability *p* was best modelled as depending on effort (Table 2), thus $p_{(\text{effort})}$ was used in the subsequent analyses.

Step 2: Temporal pattern of survival

Temporal effects as well as the effects of age and sex were determined using a set of 86 models. Φ was either kept constant across the year, fully time-dependent (i.e. separate survival rates estimated for each re-encounter interval) or stage-dependent (i.e. separate survival rates estimated for each stage; Table 1 and descriptions above). Under constant Φ, all additive combinations between age, year and sex were included (i.e. 8 models). Models with time-dependent Φ included all 18 combinations of age, year, sex and, where applicable, the interactions time x year and time x age. Similarly, 18 combinations were run with stage-dependent Φ (instead of time-dependent Φ) and thus, with the interactions stage x year and stage x age (instead of time x year and time x age). To test if a potential age effect diminished with time, models including intermediate age effects (i.e. separate age effects for the first one to four stages) were also included for stage-dependent models. As with the stage-dependent models including separate age effects for all five stages, all combinations between intermediate age-effects, year, sex and, where applicable, the interactions stage x year and stage x intermediate age-effect were included in the analysis (i.e. a total of 42 intermediate age-models).

Step 3: Stages contributing to the between-year effect

The previous analytical step revealed considerable variation between years (Table 3). The third step determined which particular stages contributed to this overall year effect. The model set for step three included the best model from step two (i.e. $\Phi_{(\text{stage + year})}\ p_{(\text{effort})}$) and the same model without any year effect. Furthermore, all 31 possible combination separately modelling additive year effects during one or several stages were included.

Step 4: Environmental factors

The analysis in the previous step showed variable winter survival between years (Table 4). Such a pattern may be due to annual differences in food availability or weather conditions. In the fourth step, four covariates were considered to explore possible correlations with year-dependent winter survival rates: the winter rodent index, mean temperature, total precipitation and the number of days with snow. To determine if any of these covariates may explain the observed year effect during winter, all 16 possible additive combinations of those four covariates were used to replace the year effect during winter in the best model from the previous analysis. The covariates may also represent a variance component in addition to the year effect during winter. Thus, models including the 16 combinations of the four covariates in addition to the year effect during winter were also considered in the *a priori* defined model set.

Carry-over effects from the nestling stage

Food supplementation

Testing for carry-over effects of experimental food supplementation during growth on survival rates during later life-history stages was based on the best model determined in step four above (i.e. $\Phi_{(\text{stage + snow})}$ $p_{(\text{effort})}$, hereafter called the baseline model). Experimental treatment may affect first year survival in two fundamentally different ways. First, the effect may diminish over time. Second, experimental treatment may differentially affect different life-history stages. To account for these two possibilities, separate treatment effects for all five stages and all possible combination were modelled. The resulting 31 models were compared to the baseline model. Models improving the baseline model by two QAIC_c units or more were considered to include an important treatment effect (Burnham & Anderson 2002; Arnold 2010).

Individual traits

Individual characteristics at fledging may also affect stage-specific survival rates. These may represent heritable quality or indirect effects of environmental factors during growth (e.g. nestling food supply). Body mass, the presence or absence of subcutaneous fat deposits under the wing, tarsus length, wing length, countenance (i.e. struggling during handling or not) and eye coloration (i.e. intense or pale) were considered for this analysis. Correlation between individual traits and the survival rates in later life-history stages were analysed analogous to the carry-over effects of experimental treatment. For each individual trait, 31 models were compared to the baseline model.

Results

MODEL SELECTION

According to the first analytical step re-encounter rates were best modelled as depending on sampling effort (Table 2). Step two of the analysis established stage-specific survival rates and an overall year effect (Table 3). The third step specified that the overall year effect resulted from annual differences in winter survival rates (Table 4). And the fourth step correlated fortnightly survival rates in winter with the duration of snow cover (Table 5). Thus, first-year survival varied amongst the life-history stages and in response to environmental conditions during winter. The results reported hereafter are based on the best model of the four-step analysis: $\Phi_{(\text{stage + snow})}\ p_{(\text{effort})}$.

RE-ENCOUNTER RATES

Fortnightly re-encounter rates were very high throughout most of the study ($p = 0.961 \pm 0.006$; estimate ± SE). During periods of reduced sampling effort re-encounter rates ranged between $p = 0.557 \pm 0.212$ and $p = 0.792 \pm 0.126$ (estimates ± SE; Fig. 1). These periods were of very short duration (i.e. only six intervals in two years; Fig. 1).

TEMPORAL PATTERN OF SURVIVAL

Stage-specific survival

Fortnightly survival rates differed among stages and ranged from 0.811 ± 0.054 to 0.981 ± 0.013 (estimates ± SE; Table 6). They were very low when little owls reared their first brood; intermediate during the dispersal stage; and high during incubation and the post-dispersal stage (Fig. 2). Winter survival rates as estimated by model $\Phi_{(\text{stage})}\ p_{(\text{effort})}$ were very similar to survival rates during the dispersal stage ($\Phi_{\text{dispersal}} = 0.947 \pm 0.011$; Table 6; $\Phi_{\text{winter}} = 0.948 \pm 0.012$; estimates ± SE).

Cumulative survival determines the proportion of individuals surviving a particular period by accounting for the duration of the period as well as period-specific survival rates. During the dispersal stage cumulative survival was low compared to other stages considered in this study (Fig. 3). About 71% of all individuals survived the dispersal stage ($\Phi_{\text{cum dispersal}} = 0.706 \pm 0.048$; estimate ± SE; Table 7). While this was comparable to cumulative survival during brood rearing ($\Phi_{\text{cum rearing}} = 0.728 \pm 0.082$; estimate ± SE; Table 7), cumulative survival was considerably higher during incubation and the post-dispersal stage. Almost 90% survived the incubation period ($\Phi_{\text{cum incubation}} = 0.883 \pm 0.056$; estimate ± SE; Table 7) and over 95% survived the short post-dispersal stage ($\Phi_{\text{cum post-dispersal}} = 0.963 \pm 0.025$; estimate ± SE; Table 7). The only stage with lower cumulative survival than the dispersal stage was winter ($\Phi_{\text{cum winter}} = 0.652 \pm 0.064$; estimate ± SE; estimated by the model $\Phi_{(\text{stage})}\ p_{(\text{effort})}$).

Predation was the main cause of mortality in this study. 81.0% of all determined casualties (*n* = 42) could be attributed to predation. During winter, predation-related mortality was even higher (91.7%; *n* = 12). Of all 167 individuals considered in this study, 45 (26.9%) survived to the end of the study.

Effect of environmental factors

Model selection showed that annual variation in overall survival originated primarily from environmental conditions during winter. Fortnightly survival rates during winter varied with the duration of snow cover (Table 5). High survival rates were detected during winter periods with no snow ($\Phi_{\text{winter with no snow}} = 0.977 \pm 0.009$; estimate ± SE; Table 6) and were then comparable to survival rates during incubation and the post-dispersal stage (Fig. 2). However, during snow-rich periods (i.e. periods with 10 days of snow cover) survival rates were very low ($\Phi_{\text{winter with 10 days of snow}} = 0.811 \pm 0.054$; estimate ± SE; Table 6), comparable to survival rates during brood rearing (Fig. 2).

While cumulative winter survival across all years was somewhat lower than that of the dispersal stage (see above), the relative importance (in terms of survival) of the winter stage varied strongly between years (Fig. 3). In comparison with the dispersal stage, cumulative winter survival was higher during winters with little snow (i.e. four days of snow cover) but much lower during snowy winters (i.e. with > 30 days of snow cover). More than 80% of young little owls survived the winter with little snow ($\Phi_{\text{cum winter 2011/12}} = 0.803 \pm 0.061$; estimate ± SE; Table 7). In contrast, only about half of them survived snowy winters ($\Phi_{\text{cum winter 2009/10}} = 0.542 \pm 0.077$; $\Phi_{\text{cum winter 2010/11}} = 0.486 \pm 0.090$; estimates ± SE; Table 7). As a consequence of variable winter conditions, cumulative survival across the entire study period also varied between years (Fig. 3). Between 21.2% and 35.1% of juvenile little owls survived from independence to the end of first reproduction.

Survival rates during winter did not correlate with other environmental factors considered (i.e. mean temperature, total precipitation, and seasonal rodent index).

CARRY-OVER EFFECTS FROM THE NESTLING STAGE

No carry-over effects from the nestling stage were found. Neither including experimental treatment nor individual covariates substantially improved the $QAIC_c$ of the model $\Phi_{(\text{stage + snow})}\ p_{(\text{effort})}$. All $\Delta QAIC_c$ were smaller than 0.625 (with a $\Delta QAIC_c \geq 2$ indicating a substantial improvement of the model). Thus, experimental food supplementation did not affect first-year survival after reaching independence. Furthermore, mortality during the study period did not vary significantly in relation to fledgling phenotype (visualized for body mass and fat deposits in Fig. 4).

Discussion

STAGE-SPECIFIC SURVIVAL

First-year survival in little owls varied over the sequence of life-history stages from dispersal to first breeding. Across the entire first year, important mortality occurred in most stages (Table 7; Fig. 3). Specifically, survival was very low during the nestling and the post-fledging stage (Chapter 2) as well as during the dispersal stage, in winter, and when birds provisioned their first brood (this study). About 30% of all individuals entering any of these stages died during that particular stage. The high mortality during rearing reported here are likely underestimated since our study did not cover the entire rearing stage. Low mortality only occurred during the post-dispersal stage and during incubation. Thus, the first year of life is marked by a cascade of different bottlenecks, leading to the overall low juvenile survival compared to the adult annual survival of c. 0.7 (van Nieuwenhuyse *et al.* 2008; Le Gouar *et al.* 2011; Thorup *et al.* 2013). However, more than half of all hatchlings died before leaving the parental territory (Chapter 2) while only one third of them died during the five stages considered in this study. While we found differential survival rates in relation to fledgling body mass and fat deposits during the early post-fledging stage (Chapter 2), we did not find any trait-related variation in survival rates in the life-history stages analysed here. The considerable mortality during later life-history stages did not result in selection for any fledgling trait considered in this study.

Overall, our result that 27.3% of all fledglings survived to first reproduction (this study and Chapter 2) is very similar to the annual survival rates of juvenile little owls estimated from a large scale ringing study. Le Gouar *et al.* (2011) reported annual juvenile survival rates of 0.258. A survival analysis combining ringing and radio-telemetry data revealed an overall similar pattern in first-year survival, although survival rates were somewhat lower (Thorup *et al.* 2013).

WINTER SURVIVAL

Survival rates in all life-history stages except winter were similar in all three years of the study. We conclude that the estimated survival rates are a characteristic of these stages. In contrast, winter survival varied considerable between years, depending on unpredictable climatic conditions. In little owls, survival rates during snow-free winter periods were among the highest throughout the first year of life (i.e. similar to the survival rates of the post-dispersal or incubation stage; Fig. 2). However, during long periods of snow cover survival rates dropped to a level comparable to the lowest rates within the first year of little owl life (i.e. during the nestling stage and during provisioning of their first brood). Thus, the high costs of the winter stage incurred mostly during the snow-rich periods. This mortality contributed much to the annual variation in first-year survival. Similar effects of periods of adverse weather condition negatively affecting winter survival were reported for other bird species (e.g. Peach *et al.* 1995; Robinson *et al.* 2004; Robinson *et al.* 2007) but in other studies no significant effects were detected (e.g. Wiktander 1998; Peach *et al.* 1999).

In conclusion, the reported high mortality in winter is not a characteristic of the life-history stage but an effect of variable environmental conditions. The severe effect of snow cover on first-year survival therefore provides one possible explanation of the latitudinal and altitudinal limitations in the geographic distribution of little owls (van Nieuwenhuyse *et al.* 2008).

FOOD AS AN IMPORTANT ECOLOGICAL FACTOR SHAPING SURVIVAL PATTERNS

Experimental food supplementation during growth has a marked positive effect on nestling survival in little owls (Thorup *et al.* 2010; Perrig *et al.* 2014). It also indirectly affects early post-fledging survival, acting via individual physical characteristics such as body mass and fat deposits (Chapter 2). This study did not detect any carry-over effects of the experimental treatment beyond the post-fledging stage. Neither experimental food supplementation during growth nor individual fledgling traits (which vary in relation to food-supply) had a considerable effect on the survival during dispersal or later life-history stages. This suggests that the effects of (increased) food supply during growth did not persist for long periods.

Low survival rates during snow-rich periods may also be driven by limitations in food supply. It has long been recognized that food is an important determinant of winter survival (Jansson *et al.* 1981; Desrochers *et al.* 1988; Peach *et al.* 1999; Robinson *et al.* 2007). For small owls, food accessibility is strongly reduced when snow covers the ground (Korpimäki 1986; van Nieuwenhuyse *et al.* 2008). However, the main cause of mortality detected in this study was predation, not starvation. Reduced food accessibility likely increases foraging time of little owls. Since they spend much time hunting on the ground (van Nieuwenhuyse *et al.* 2008) a blanket of snow defeats the camouflage of little owls when hunting, leading to an increased predation risk. Furthermore, snow-rich periods may cause other predators of rodents (e.g. common buzzard, *Buteo buteo*; tawny owls *Strix aluco*; red foxes, *Vulpes vulpes*) to switch to alternative prey species (including little owls). The predation risk may also be increased because of reduced vigilance or slower reaction time of food-deprived individuals (Powell 1974; Jones *et al.* 2009). The combination of increased time at increased predation risk may have resulted in low survival rates during snow-rich periods.

Survival rates were not only low in times of reduced food accessibility (i.e. during snow-rich periods) but also when energy demand was high (e.g. when young parents raise their own juveniles; Martin 1987). We conclude that short-term effects of food supply on survival are important throughout the entire first year of life of little owls. Limited food supply has immediate effects on survival but these effects do not carry over far beyond the period of food limitation. Adopting the terminology from breeding biology (Drent & Daan 1980; Stephens *et al.* 2009), we suggest that first-year little owls are ‘income survivors’ rather than ‘capital survivors’.

IS NATAL DISPERSAL COSTLY?

Elevated costs during natal dispersal (e.g. Bowler & Benton 2005; Benard & McCauley 2008; Barton *et al.* 2012; Bonte *et al.* 2012; Hardouin *et al.* 2012) suggest that the dispersal stage is a major bottleneck in avian life-histories. Our results show that in little owls there were indeed high costs (in terms of survival rates) associated with this stage. Almost one third of the departing juvenile little owls died during the dispersal stage. The few other studies empirically estimating the costs of dispersal compared survival rates of philopatric and dispersing individuals. These studies found similar (e.g. Byrom & Krebs 1999) or lower costs of dispersal (e.g. van Vuren & Armitage 1994). While other life-history stages of little owls bore similar costs (see discussion above), most individuals died during the nestling and post-fledging stages (32.5% and 20.3% of all hatchlings, respectively; Fig. 3). Overall, in little owls the dispersal stage certainly contributed towards the critical life-history bottleneck during the first year of life, but it was neither the only nor the most severe factor.

The mechanism behind the considerable mortality during dispersal remains unclear. The results of this study showed that neither food supply during development nor timing of breeding affected survival during the dispersal stage. The lack of annual variation of survival during the dispersal stage suggests that year-dependent variables (e.g. weather conditions, food availability) are not major determinants of survival during natal dispersal in little owls. Furthermore, survival rates during natal dispersal did not correlate with any of the six fledgling traits considered in this study. These traits represent different potential mechanisms affecting survival during dispersal. For example, wing length is closely related with flight capacity (Pennycuick 2008), tarsus length is a measure of structural size in birds (Senar & Pascual 1997), fat deposits represent primarily energy stores (Jenni & Jenni-Eiermann 1998) and eye colour is linked to nutritional quality (Oliphant 1987; Hill & McGraw 2006) and may affect intraspecific interactions (Newton & Marquiss 1982; Bortolotti *et al.* 2003; Guillemain *et al.* 2012). Thus, our results suggest that neither the energetic state of young little owls at fledging, nor their size, flight capacity, nutritional condition or behavioural disposition was linked to survival during the dispersal stage. In addition, there was no difference in survival between males and females, although female little owls typically settle further away from their natal site (van Nieuwenhuyse *et al.* 2008). More detailed investigations of the survival patterns during the dispersal stage (i.e. before departure and during transience and settlement), of dispersal distance and duration, and of movement patterns through a habitat matrix will probably reveal more of the mechanism behind the costs of dispersal in little owls (e.g. Yoder *et al.* 2004).

In little owls, first year survival is characterized by a cascade of several bottlenecks, differing in the underlying mechanisms. Consistent with the general assumption of elevated costs during natal dispersal (e.g. Benard & McCauley 2008; Bonte *et al.* 2012; Hardouin *et al.* 2012) our results show that the dispersal stage in little owls makes an important and consistent contribution towards low first-year survival. However, further research on ecological determinants (e.g. habitat matrix, food supply, social factors) of the cost and benefits of natal dispersal is needed to fully understand the fitness-relevance of the sequence of life-history stages from hatching to first reproduction (Bowler & Benton 2005).

Food supply during growth (Chapter 2) and annual variability of winter weather (affecting food availability) were two environmental factors affecting variation in the proportion of juveniles surviving to first reproduction and thus, influenced parental reproductive output. Thus, our results underline that trophic interactions are likely an important part of the fitness-relevant mechanisms throughout many stages of the first year of life. Continuous food accessibility throughout the first year of life is thus crucial for the survival of an ‘income survivor’ like the little owl.

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Table 1. Description of the five stages used in the analysis. The time period, the number of fortnightly re-encounter intervals and the characteristics of each stage are given.

Stage	Period	Nb. of intervals	Stage characteristics
Dispersal	1 Aug – 24 Oct	6	Pre-dispersal excursions and main dispersal
Post-dispersal	24 Oct – 21 Nov	2	Period between dispersal and winter
Winter	21 Nov – 13 Mar	8	Adverse climatic conditions, establishing breeding territories and pair formation
Incubation	13 Mar – 22 May	5	Egg-laying and incubation
Brood rearing	22 May – 19 Jun	2	Rearing hatchlings of the first brood

Table 2. Results of the model selection for re-encounter rates *p*. Survival was modelled as $\Phi_{(\text{time + year + age + sex + time x year + time x age})}$. Model selection shows that *p* is best modelled as depending on sampling effort. Results are adjusted for small sample size and overdispersion ($\hat{c} = 1.872$). $\Delta QAIC_c$ is the difference in $QAIC_c$ in reference to the best model.

Model	$QAIC_c$	$\Delta QAIC_c$	Num. Par.	QDeviance
$p_{(\text{effort})}$	968.5040	0	97	765.1935
$p_{(\text{effort + year})}$	969.5761	1.0721	99	761.8702
$p_{(\text{year})}$	1016.7303	48.2263	96	815.6143
$p_{(.)}$	1017.7356	49.2316	94	821.0021

Table 3. Results of the ten best models of model selection among the 86 models assessing which factors affected the temporal patterns of first year survival. Re-encounter rates *p* were modelled as effort-dependent. The digits behind the additive factor 'age' in a model name designate the stages over which a single age effect was modelled (i.e. 1 = dispersal, 2 = post-dispersal, 3 = winter, 4 = incubation and 5 = brood rearing). For example, in the model $\Phi_{(\text{stage + year + age 1-3})}$ an age effect was included for the stages 1-3. The results revealed stage-specific survival rates and an overall year effect. Results are adjusted for small sample size and overdispersion ($\hat{c}$ = 1.872). $\Delta QAIC_c$ is the difference in $QAIC_c$ in reference to the best model.

Model	$QAIC_c$	$\Delta QAIC_c$	Num. Par.	QDeviance
$\Phi_{(\text{stage + year})}$	856.7853	0	11	834.6612
$\Phi_{(\text{stage + year + age 1-2})}$	858.3771	1.5918	12	834.2304
$\Phi_{(\text{stage + year + sex})}$	858.4574	1.6721	12	834.3107
$\Phi_{(\text{stage + year + age 1})}$	858.4603	1.6750	12	834.3136
$\Phi_{(\text{stage + year + age 1-5})}$	858.5227	1.7374	12	834.3760
$\Phi_{(\text{stage + year + age 1-3})}$	858.5471	1.7618	12	834.4004
$\Phi_{(\text{stage + year + age 1-4})}$	858.6720	1.8867	12	834.5254
$\Phi_{(\text{stage})}$	859.5978	2.8125	9	841.5132
$\Phi_{(\text{stage + year + age 1-2 + sex})}$	860.0921	3.3068	13	833.9209
$\Phi_{(\text{stage + year + age 1 + sex})}$	860.1709	3.3856	13	833.9997

Table 4. Results of the ten best models of model selection among the 33 models determining which stage contributed to the overall year effect. Re-encounter rates *p* were modelled as effort-dependent. The digits behind the additive factor ‘year’ in a model name designate for which stages a separate year effect was modelled (i.e. 1 = dispersal, 2 = post-dispersal, 3 = winter, 4 = incubation and 5 = brood rearing). For example, in the model $\Phi_{(\text{stage + year 235})}$ a separate year effect was included for stages 2, 3 and 5. No digit is given if a single year effect over the entire study period was included (i.e. model $\Phi_{(\text{stage + year})}$). The results revealed that the major between-year variation occurred during winter. Results are adjusted for small sample size and overdispersion ($\hat{c} = 1.872$). ΔQAIC_c is the difference in QAIC_c in reference to the best model.

Model	QAIC_c	ΔQAIC_c	Num. Par.	QDeviance
$\Phi_{(\text{stage + year 3})}$	852.9395	0	11	830.8154
$\Phi_{(\text{stage + year 23})}$	853.8413	0.9018	13	827.6701
$\Phi_{(\text{stage + year 34})}$	856.2000	3.2605	13	830.0288
$\Phi_{(\text{stage + year})}$	856.7853	3.8458	11	834.6612
$\Phi_{(\text{stage + year 13})}$	856.8154	3.8759	13	830.6442
$\Phi_{(\text{stage + year 35})}$	856.8919	3.9524	13	830.7207
$\Phi_{(\text{stage + year 234})}$	857.1087	4.1692	15	826.8828
$\Phi_{(\text{stage + year 123})}$	857.7558	4.8163	15	827.5298
$\Phi_{(\text{stage + year 235})}$	857.8013	4.8618	15	827.5754
$\Phi_{(\text{stage})}$	859.5978	6.6583	9	841.5132

Table 5. Results of the ten best models of model selection among the 32 models assessing which factors affected winter survival rates. Re-encounter rates *p* were modelled as effort-dependent. All additive factors were only included for the winter stage. Snow was the most important factor explaining variation in winter survival rates. Other factors (i.e. year, total precipitation, mean temperature and a winter rodent index) did not substantially improve the model. Results are adjusted for small sample size and overdispersion ($\hat{c}$ = 1.872). $\Delta QAIC_c$ is the difference in $QAIC_c$ in reference to the best model.

Model	$QAIC_c$	$\Delta QAIC_c$	Num. Par.	QDeviance
$\Phi_{(\text{stage + snow})}$	845.5119	0	10	825.4086
$\Phi_{(\text{stage + snow + precipitation})}$	845.5242	0.0123	11	823.4001
$\Phi_{(\text{stage + snow + rodents})}$	846.6227	1.1108	11	824.4987
$\Phi_{(\text{stage + snow + precipitation + temperature})}$	846.7931	1.2812	12	822.6464
$\Phi_{(\text{stage + snow + precipitation + rodents})}$	847.0677	1.5558	12	822.9210
$\Phi_{(\text{stage + snow + temperature})}$	847.2602	1.7483	11	825.1362
$\Phi_{(\text{stage + snow + year})}$	848.1592	2.6473	12	824.0125
$\Phi_{(\text{stage + snow + precipitation + temperature + rodents})}$	848.2546	2.7427	13	822.0834
$\Phi_{(\text{stage + snow + temperature + rodents})}$	848.2587	2.7468	12	824.1120
$\Phi_{(\text{stage + snow + year + precipitation})}$	848.9123	3.4004	13	822.7410

Table 6. Fortnightly survival rates for the five stages used in the study as estimated with the model $\Phi_{(\text{stage + snow})}\ p_{(\text{effort})}$. Predicted winter survival rates are given for intervals with no or 10 days of snow cover. For comparison, fortnightly survival rates during the nestling stage and the four following post-fledging intervals (i.e. post-fledging 1-4) as determined in chapter two were also included. A classification in relation to the dispersal stage is also given.

	Fortnightly survival rate				Survival rate in relation to the dispersal stage
Stage	Estimate	SE	95% CI		
Nestling	0.822	0.0256	0.766	0.866	Low
Post-fledging 1	0.853	0.0301	0.784	0.903	Low
Post-fledging 2	0.901	0.0275	0.833	0.943	Low
Post-fledging 3	0.942	0.0226	0.878	0.974	Equal
Post-fledging 4	0.965	0.0192	0.901	0.988	High
Dispersal	0.947	0.0107	0.919	0.961	-
Post-dispersal	0.981	0.0127	0.931	0.995	High
Winter periods with no days of snow cover > 3cm	0.977	0.0088	0.951	0.989	High
Winter periods with 10 days of snow cover > 3cm	0.811	0.0537	0. 683	0. 895	Low
Incubation	0.975	0.0124	0.935	0.991	High
Brood rearing	0.853	0.0483	0.732	0.925	Low

Table 7. Stage-specific cumulative survival rates as calculated with the survival estimates from the model $\Phi_{(\text{stage + snow})}$ $p_{(\text{effort})}$. Year-specific winter survival is given. For comparison, cumulative survival of the nestling stage (i.e. two fortnightly intervals) and the early post-fledging stage (i.e. post-fledging survival rates 1-4) as determined in chapter two is also included. A classification in relation to the dispersal stage is also given. The standard error and 95% confidence intervals of cumulative survival were determined using the delta method (Powell 2007) and the beta distribution, respectively.

	Stage-specific cumulative survival				Survival in relation to the dispersal stage
Stage	Estimate	SE	95% CI		
Nestling	0.675	0.042	0.590	0.755	Equal
Post-fledging	0.699	0.039	0.620	0.773	Equal
Dispersal	0.706	0.048	0.608	0.796	-
Post-dispersal	0.963	0.025	0.901	0.995	High
Winter 2009/10	0.542	0.077	0.391	0.690	Low
Winter 2010/11	0.486	0.090	0.312	0.661	low
Winter 2011/12	0.803	0.061	0.671	0.908	high
Incubation	0.883	0.056	0.753	0.968	high
Brood rearing	0.728	0.082	0.553	0.872	equal

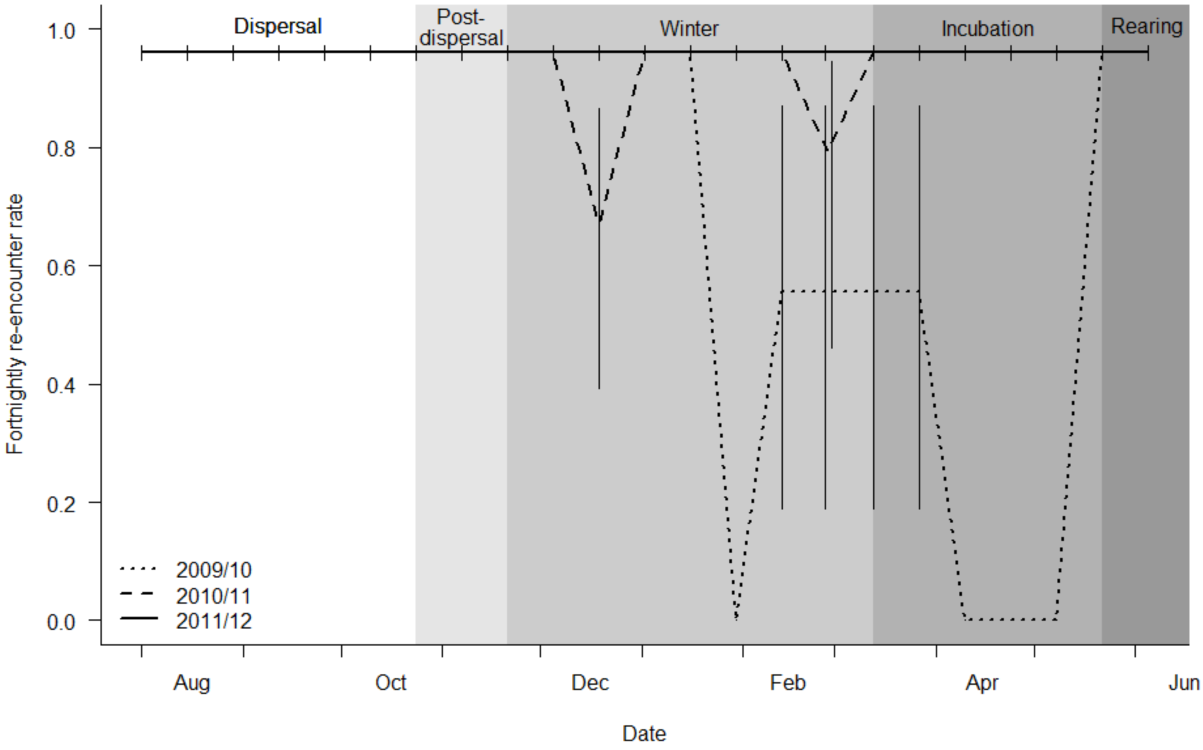

Fig. 1. Re-encounter rates *p* of radio-tagged juvenile little owls in relation to sampling effort. Vertical solid lines represent the 95% CI. Sampling effort was reduced during four consecutive intervals in early spring 2009/10 and during two separate intervals in winter 2010/11. Birds were not tracked during one interval in winter 2009/10 and three consecutive intervals in spring 2010.

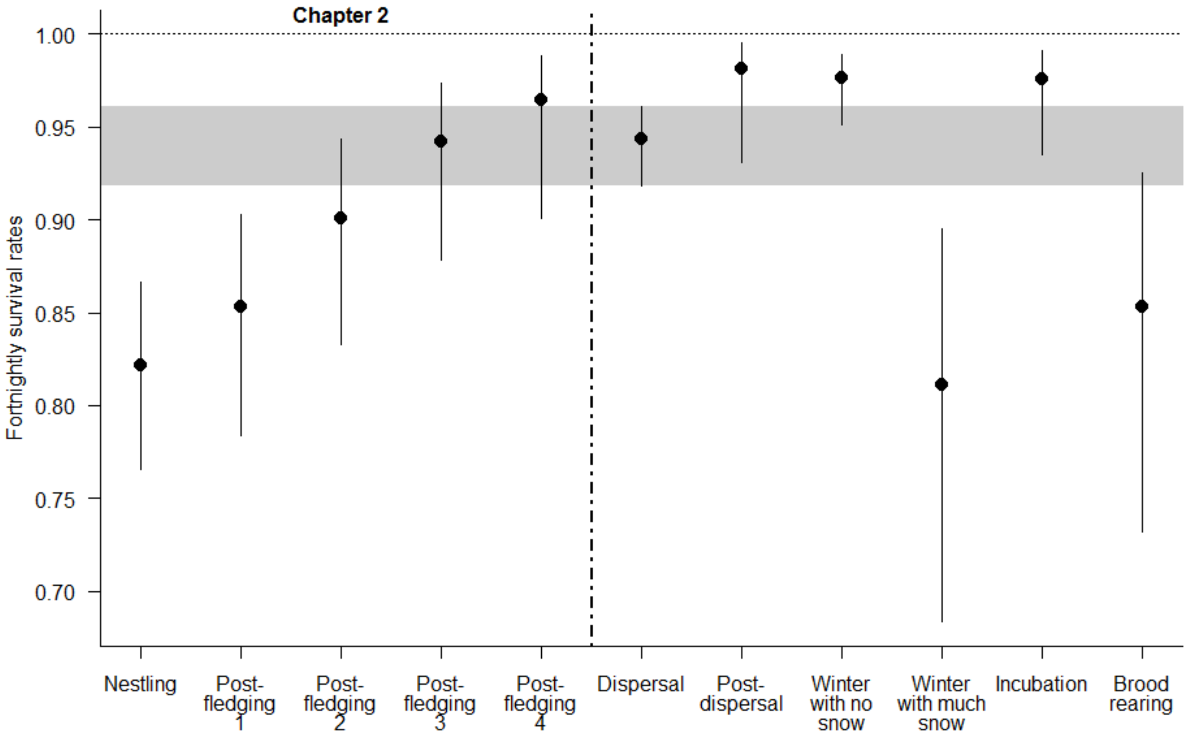

Fig. 2. Fortnightly survival rates of young little owls in different life-history stages. Estimates for dispersal, post-dispersal, winter periods (with no days and with 10 days of snow cover), incubation and brood rearing were calculated with the model $\Phi_{(\text{stage + snow})}\ p_{(\text{effort})}$. For comparison, fortnightly survival rates during the nestling stage and the four subsequent post-fledging intervals (i.e. post-fledging 1-4) as determined in chapter two were drawn on the left-hand side of the vertical dash-dotted line. Vertical lines represent the 95% CI. The grey bar represents the 95% CI of the dispersal stage to facilitate comparison. Survival rates during the dispersal stage were reduced compared to most later life-history stages. However, survival rates were particularly low during long periods of snow cover, during brood rearing and during the nestling and very early post-fledging periods.

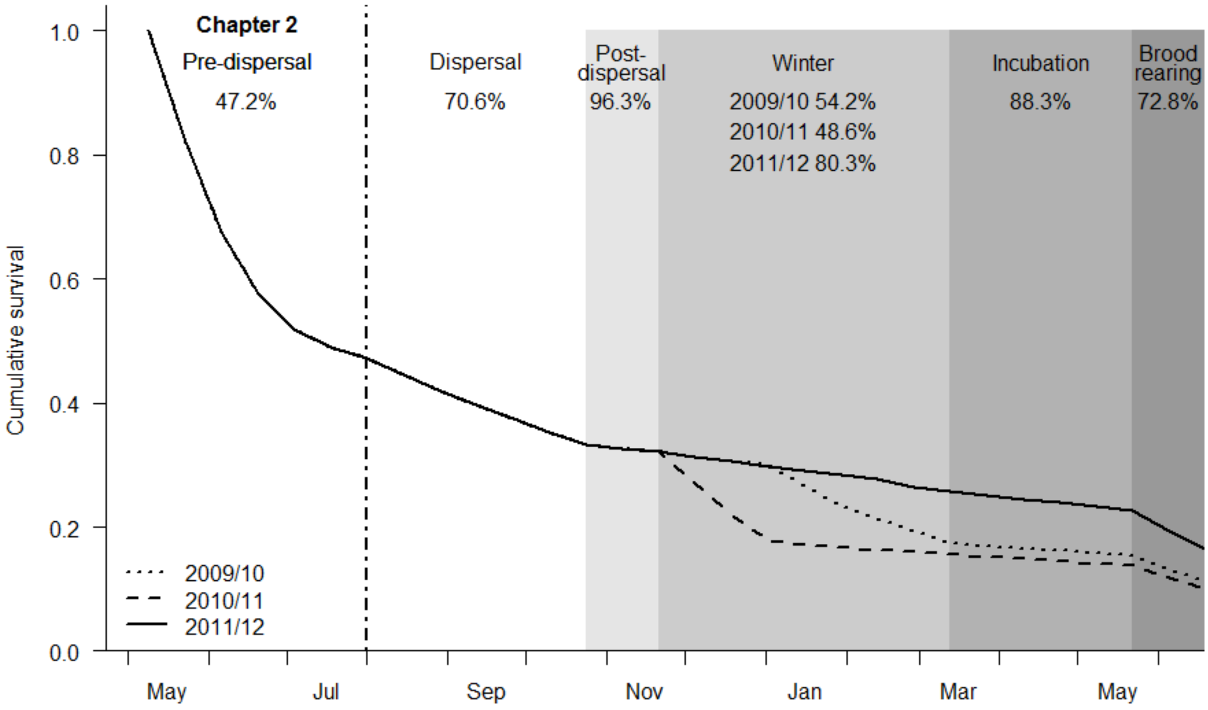

Fig. 3. Cumulative survival of little owls from hatching to first reproduction. Cumulative survival was calculated from the fortnightly survival rates of chapter two (pre-dispersal stage; left-hand side of the vertical dash-dotted line) and the estimates from the model $\Phi_{(\text{stage + snow})}$ $p_{(\text{effort})}$ (remaining stages; this study). Stage-specific cumulative survival (i.e. the percentage of individuals surviving a particular stage) is indicated below the name of the stage. Cumulative survival is particularly low during the pre-dispersal period and during snow-rich winters (i.e. winters 2009/10 and 2010/11). Annual differences in winter survival lead to annual differences in recruitment rates.

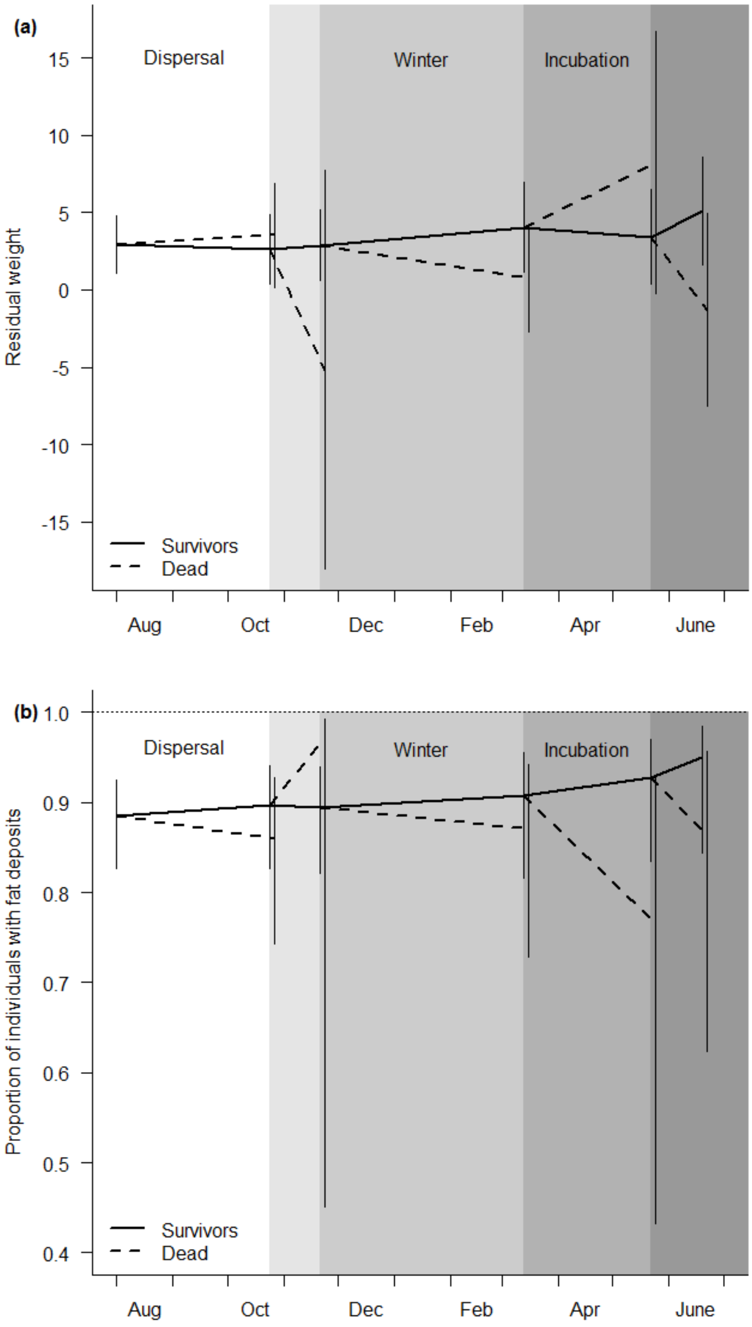

Fig. 4. Individual fledgling traits of young little owls dying during (dashed line) and surviving (solid line) the different stages from dispersal to first reproduction. The traits represented here are (a) the residual body mass and (b) the proportion of individuals with fat deposits. Vertical lines represent the 95% CI. The lack of a clear trend over time for both traits indicates that mortality during the different stages was random with respect to the traits.

CHAPTER 4

Roost site selection by little owls (*Athene noctua*) in relation to environmental conditions and life-history stages

Anja Bock, Beat Naef-Daenzer, Herbert Keil, Fränzi Korner-Nievergelt, Marco Perrig &
Martin U. Grüebler

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Abstract

Roost site selection is a state-dependent process, affected by the individual's costs and benefits of roosting at a specific site in the available environment. Costs and benefits of different roost sites vary in relation to intrinsic factors and environmental conditions. Thus, the cost–benefit functions of roost sites are expected to differ between seasons and life-history stages, resulting in adjustments in roost site selection. Studying roost site selection throughout the year therefore provides information about year-round habitat requirements at different life-history stages. However, little is known about the roosting behaviour of birds. Here, the roost site selection of little owls (*Athene noctua*) was studied by repeated daytime location of 24 adult and 75 juvenile radio-tagged individuals from July to November. Little owls preferred sheltered roost sites such as tree cavities with multiple entrances. They increasingly used sheltered sites from summer to winter and preferentially used sheltered roost sites with low ambient temperatures. Juveniles used significantly less sheltered sites during dispersal than before and afterwards, and used less sheltered sites than adults within their home-range. The survival probability of birds roosting frequently at exposed sites was reduced. Roost site selection is probably driven by the two mechanisms of predator avoidance and thermoregulation, and the costs of natal dispersal may include increased predation threat and higher energy expenditure for thermoregulation. We suggest that adequate roost sites, such as multi-entrance tree cavities, are an important habitat requirement for little owls and that habitat quality can be affected by manipulating their availability.

Keywords

Habitat quality, habitat selection, natal dispersal, roosting behaviour, tree cavity use.

Introduction

Birds often spend large parts of the day or night at their roosts. Thus, roost site selection is likely to be an important determinant of individual fitness (Lack 1968). In a life-history context, roost site selection should have evolved as a product of the costs and benefits of roosting at different sites (Sunde *et al.* 2003). For example, any energetic cost associated with choosing and occupying a roost site will reduce the energy available for reproduction and self-maintenance. When selecting a roost site, natural selection will favour individuals that optimize the cost–benefit functions of potential sites. Roost site selection can be influenced by predation risk (Thiel *et al.* 2007; Tillmann 2009), parasite occurrence (Christe *et al.* 1994; Rohner *et al.* 2000), disturbance probability (Peters & Otis 2007) and thermal properties (Kendeigh 1961; Buttemer 1985; Walsberg 1986).

Predator avoidance during roosting should result in preferences for sites inaccessible to most predators, offering escape routes, or enabling detection of approaching predators (Thiel *et al.* 2007). Sheltered or enclosed roost sites may be invisible and inaccessible to large predators (Drent 1987; Mainwaring 2011). However, specialist predators often search roost sites for prey, increasing predation risk for birds roosting in predictable sites (Dhondt *et al.* 2010). Open roost sites may allow more effective predator detection and escape response (Walsberg & King 1980) but may be more costly if predation risk is increased and the energetic costs of escape behaviour are high. Thus, the benefits of different sites are likely to be species-specific and dependent on the local predator community.

By selecting roost sites that minimize thermoregulatory costs, birds may reduce their energy requirements or re-allocate conserved energy to other vital processes (Walsberg 1986; Wolf & Walsberg 1996). Studies of the thermal benefits of avian roost sites show that during the non-breeding season, nestboxes and other cavities offer significant thermal benefits to small passerines (Kendeigh 1961) and barn owls *Tyto alba* (McCafferty *et al.* 2001). Birds roosting in nestboxes, buildings or tree cavities may save over 10% of their energy expenditure by reducing their metabolic heat production due to higher temperatures, better insulation and shielding from wind (McCafferty *et al.* 2001; Paclík & Weidinger 2007; Mainwaring 2011). Even slight shielding from wind can have large positive thermoregulatory effects (Wiersma & Piersma 1994; Wolf & Walsberg 1996). Moreover, roost site temperature may affect energy saving strategies such as rest-phase hypothermia (Nord *et al.* 2011).

In seasonal environments, the cost–benefit functions of roost sites are expected to differ between seasons due to both environmental changes affecting roost site characteristics and the changing requirements of birds. For example, thermal benefits may be more important in winter because birds have higher thermoregulatory costs or lower energy intake (McCafferty *et al.* 2001). Moreover, vegetational changes such as the fall of tree leaves in autumn might alter the benefits of a predation avoidance strategy employed in the summer, and predation pressure might be higher in winter when food resources for predators are scarce.

Roost site selection may also vary between different life-history stages. In particular, for juveniles leaving the parental home-range, costs and benefits of roost sites might differ from those of adults, because juveniles are inexperienced and must survive in unknown habitats during the natal dispersal period (Clobert *et al.* 2001). One of the main costs of dispersal is increased mortality risk when crossing unsuitable habitats or searching for future breeding sites in suitable but unknown habitats. Low availability or accessibility of high-quality roost sites in these habitats might be an important cause of increased mortality risk during dispersal. However, little is known about roost site selection during this life-history stage.

For all the reasons discussed above, the availability of adequate roost sites may be an important aspect of habitat quality, and understanding roost site selection as a component of habitat use throughout the year and across life-history stages provides a crucial link between behavioural ecology and conservation biology. However, investigation of roost site selection is still rare in avian habitat selection studies. This is partly because the identification of roost sites is difficult without modern tagging techniques. In particular, the roosting behaviour of birds in the non-breeding season and of non-territorial 'floating' individuals remains generally unknown.

We investigated the roosting behaviour of the little owl (*Athene noctua*), a cavity-nesting nocturnal bird species that in central Europe occupies open, semi-open and agricultural landscapes. In recent decades, it has been declining in numbers (van Nieuwenhuyse *et al.* 2008) and in many areas it now persists due to the provision of artificial nestboxes. In recent years, some populations have increased again after the provision of artificial nestboxes as a large-scale conservation measure (Exo 1992; Newton 1994). Our aims were (i) to identify preferred roost sites of adult and juvenile little owls in their home-ranges; (ii) to investigate roost site selection in relation to ambient temperature and across seasons; (iii) to assess the use of sheltered sites, in particular by juveniles after leaving their natal home-range; and (iv) to assess whether roosting at open sites has survival costs. We predicted that sheltered roost sites such as tree cavities would be preferred for thermoregulatory reasons, and that the use of sheltered sites would increase at low temperatures. Moreover, stronger selection of sheltered sites in winter, irrespective of temperature, was expected due to environmental changes such as the fall of tree leaves, which may increase detection by predators or mobbing birds. After independence, we predicted that sheltered sites would be used less frequently by juvenile little owls during autumnal dispersal than by adult birds in their known home-ranges.

Materials and methods

STUDY SPECIES AND STUDY AREA

In central Europe, little owls occur mainly in open habitats with widely spaced trees. Typical secondary habitats are traditionally cultivated areas with large orchards. Foraging takes place in open and highly structured habitats where little owls feed on insects, small mammals, earthworms and reptiles. Juveniles fledge between May and July and leave the parental home-range in early September the same year.

The study area was located in southwest Germany in the district of Ludwigsburg (48°53’43″N, 9°11’45″E). The agricultural landscape includes orchards, vineyards and arable farmland. The study population comprises 10 subpopulations with a total of approximately 220 breeding pairs in an area of 250 km^2 (distances between subpopulations: 5–20 km; H. Keil unpubl. data). Daily mean temperature and precipitation for the study area were obtained from the meteorological station at Stuttgart-Echterdingen (Germany, station ID: 4931), just south of the study area.

RADIO-TAGGING AND TRACKING OF ROOSTING INDIVIDUALS

In spring 2010, 137 little owls (18 females, 14 males, 105 juveniles) were tagged with very high frequency (VHF) radio-transmitters of our own construction (Naef-Daenzer *et al.* 2005). Juveniles were taken from nestboxes at around day 30. Adult birds were caught in the second half of the nestling period by mist-netting near the nestbox. The transmitters weighed 6.9–7.2 g (i.e. 4–5% of the birds’ body mass) and had an expected lifespan of approximately 400 days. The tags were fitted with a standard figure-8 harness (Kenward 2001). Survival probabilities and reproductive output of radio-tagged birds were comparable to estimates in other studies, indicating no adverse effects of the marking in our study (unpubl. data). This was also corroborated by recent telemetry studies of little owls (Sunde *et al.* 2009; Thorup *et al.* 2013). Individuals were located at least once each week during daylight hours from mid-

July to the end of November 2010. After triangulation, we approached the bird's roost site until the exact location was identified. Trees were scanned using binoculars from distance at first, often resulting in visual identification if the bird roosted in an exposed site in the crown. If this was not the case, we looked for cavities in the tree and approached closer to identify the use of cavities. By using this approach, we minimized escape of birds from their roost. Seven categories of roost sites were recorded: fruit tree crown, other tree crown, building, nestbox, stack of wood, tree cavity with one entrance, tree cavity with more than one entrance. Locations were classified into three time periods: summer (mid-July to end of August; period of post-fledging dependence), autumn (beginning of September to end of October; period of natal dispersal), winter (November; period of winter home-ranges). All birds were also located one to three times a week during the night when they did not use roosts. Birds found dead were classified as predated by raptors or not (see also Sunde *et al.* 2003).

ROOST SITE AVAILABILITY

We mapped available roost sites in little owl breeding home-ranges for comparisons with roost site use. No estimates were made for dispersing individuals. Thus, comparisons were possible for all time periods in adult birds but only for the summer period in juveniles. Surveys of roost site availability were carried out between mid-September and mid-November 2010. A standardized mapping area was constructed by calculating the centroid of the roost site locations of all individuals of an owl family. Available roosts were counted within a radius of 220 m of the centroid (15.21 ha). Within each home-range, the inventory of all potential roost sites included the number of tree crowns, buildings, nestboxes, stacks of wood and tree cavities with one or more entrances. Because little owls used very different tree crowns for roosting, we counted all tree crowns in the mapping area. Buildings were only considered if they held openings that the birds could enter. Wood stacks were only considered if they had dimensions over 1 x 1 x 1 m. Tree cavities were counted if the entrance diameter was larger than 6 cm and if the depth was more than 20 cm.

STATISTICAL ANALYSIS

Measures of roost site preferences compare the use of roost sites with roost site availability. Investigating the variation in roost site preference in relation to environmental factors requires quantification of roost site use in relation to these factors to be compared with availability of roost sites within the home-range. Thus, availability of roost sites was recorded once per home-range, but roost site use was measured several times per individual and for several individuals living in the same home-range (i.e. in the same family). In a first analysis of roost site use, we fitted a multinomial logistic regression model allowing for a multinomial response variable (roost site types; Ntzoufras 2009). To account for the non-independence of observations from the same individual and from individuals living in the same home-range, we included individual and home-range as random factors. We combined the two factors age and season into a four-factor ‘period’ (juvenile summer, adult summer, adult autumn, adult winter) and included this as a fixed factor and ambient temperature as a covariate in the model. Results of this multinomial model allowed prediction of the proportional use of each roost site type in different periods and at varying temperatures. The parameters of the multinomial logistic regression model were estimated in a Bayesian framework using Markov chain Monte Carlo (MCMC) simulations in WinBUGS (Spiegelhalter *et al.* 2003), where WinBUGS was used from within R 2.13.2. (R Development Core Team 2011) using the package R2WinBUGS (Sturtz *et al.* 2005). Two Markov chains were simulated, each of length 200 000. The burn-in was set to 100 000 and the chain was thinned by 100 to save work space and reduce autocorrelation. Convergence was assessed graphically and by the R-hat value (Brooks & Gelman 1998).

Thereafter, roost site preference was estimated using the Jacobs' preference index D (Jacobs 1974). This index compares the use of a resource with its availability, providing a deeper insight into the importance of a resource than just quantifying the rate of use (Manly *et al.* 2002). The Jacobs' index $D = (u - a) / (u + a - 2ua)$ where u is the used proportion of a specific roost site type, and a is the available proportion of this roost site type. D can take values between 1 and +1. $D = 1$ means that the roost site type is completely avoided, whereas $D = 1$ means it is used exclusively. $D = 0$ corresponds to no preference (i.e. use is proportional to availability). We calculated the Jacobs' preference index in each home-range by 'period' along a gradient of temperature values based on the predicted values for roost site use from the multinomial model and the availability. Finally, the Jacobs' preference indices were averaged over all home-ranges by 'period' and temperature. The derivation of the Jacobs' preference indices including credible intervals (the Bayesian equivalent of confidence intervals) was also done in WinBUGS. The Markov chains were saved to extract their means as estimates and the 2.5 and 97.5% quantiles to describe the 95% credible intervals (95% CrI; Gelman *et al.* 2004).

Roost sites were then categorized as sheltered (inside buildings, nestboxes, wood stacks and tree cavities) or open (tree crowns). This binary variable (sheltered = 1; open = 0) was used as response variable in a generalized linear mixed model (glmer) with a binomial error distribution (i.e. logistic regression) to investigate factors affecting use of sheltered roost sites. Because individuals were located more than once and juveniles and adults of the same family used the same area, we entered individual and family as random effects. The models included the effects of season (summer, autumn, winter), precipitation (covariate), temperature (covariate) and the age of birds (adult/juvenile) as fixed effects. To test for differences in the use of sheltered sites among age classes, we included all two-way interactions with age. Thereafter, in a stepwise process, non-significant interactions were excluded.

To assess whether roosting at open sites might have survival consequences for little owls, we classified the predicted use of sheltered roost sites by adults and juveniles in the different periods into three roosting classes: infrequent use (probability of using a sheltered site < 0.4), regular use (probability 0.4–0.6) and frequent use (probability > 0.8) of sheltered roost sites. We estimated weekly apparent survival of adults and juveniles in the three roosting classes based on all locations, i.e. based on locations in the night and during the day. Ninety-eight survival histories (24 adults, 74 juveniles) were available, all starting at the same time (July 15). Encounter probability of radio-tagged little owls was close to 1 (own unpubl. data). Thus, we refrained from considering differences in encounter probabilities. We used an autoregressive formulation of a survival model to estimate weekly survival for each of the three roosting classes. The state $z_{i,t}$ (1 if the individual *i* was alive at week *t* and 0 if dead) was assumed to be Bernoulli-distributed with the probability $S_{i,t}*z_{i,t-1}$, where $S_{i,t}$ was the weekly apparent survival probability during the roosting class of individual *i* at week *t*. The model was fitted to the data using Markov chain Monte Carlo simulations in WinBUGS. The means of the simulated values were used as apparent survival estimates; the 2.5 and 97.5% quantiles were used as lower and upper limits of the 95% CrI. Survival of exposed roosting birds might be reduced during daytime, when the main predators are birds of prey. Thus, for each roosting class, we quantified the proportion of birds that died due to avian predation.

Results

ROOST SITES

A total of 1223 little owl locations were recorded between mid-July and end of November 2010, including 318 roost sites of adults and 905 roost sites of juveniles (Table 1). Little owls used open (42%) as well as sheltered sites (58%) for roosting. Roost sites were in or on trees in 84% of cases and apple trees were the most frequently used tree species (apple: 45%; pear: 18%; cherry: 2%; other tree species: 15%). Nearly one-third of roosting sites (29%) were in fruit tree cavities. Nestboxes (17%), stacks of wood (10%) and small buildings (2.5%) were also used. During the period of post-fledging dependence, little owls roosted most often within fruit tree crowns, in tree cavities with multiple entrances, in nestboxes and in wood stacks (Fig. 1). When roosting in sheltered sites, juveniles used tree cavities more frequently than adults, whereas adults used wood stacks more frequently than juveniles (Fig. 1, Table 2). The Jacobs' preference indices based on the multinomial logistic regression model results (for parameter estimates, see Supporting Information Table S1) show that little owls used tree crowns less than expected from their availability, buildings and tree cavities with one entrance according to their availability, and nestboxes, tree cavities with multiple entrances and wood stacks more frequently than expected from their availability (Fig. 1 & 2).

EFFECTS OF TEMPERATURE AND SEASON

Temperature was associated with use of sheltered roost sites (Table 3) and preference indices (Fig. 2). Sheltered sites were used more frequently at lower temperatures (Fig. 3). In particular, preference for tree cavities with multiple entrances and for wood stacks increased at low temperatures and preference for fruit tree crowns decreased significantly (Fig. 2). In frosty weather conditions, more than 80% of adults and more than 50% of juveniles roosted in sheltered sites. Precipitation had no effect on roost site selection (Table 3). Irrespective of temperature, roost site selection and preference indices differed between seasons (Fig. 2 & 4, Table 3). Adult owls increasingly used sheltered sites (Fig. 4) and tree cavities (Fig. 2, Table 2) as the season progressed from summer to winter.

EFFECT OF LIFE-HISTORY STAGE

Roost site use showed a significant interaction between age class and season (Table 3). In summer home-ranges, adults and juveniles showed no difference in selection of sheltered roost sites. However, dispersing juveniles showed less use of sheltered sites from summer to autumn, whereas adults remaining in their home-range showed increased use of sheltered sites (Fig. 4). Thus, the natal dispersal period of juveniles (autumn) was characterized by an increased use of open sites, decreasing again to the summer level after settlement in a winter home-range. However, even in winter, juvenile use of sheltered roost sites was lower than that of adults. Both age classes used tree cavities more in winter than in summer when roosting in sheltered sites (Table 2). In contrast, juveniles almost ceased to use nestboxes in winter, whereas nestbox use by adults remained constant throughout the year (Table 2).

SURVIVAL IN RELATION TO ROOSTING BEHAVIOUR

Of the 98 individuals tracked after mid-July, 25 individuals were recorded dead during the 25 weeks of the study. Weekly apparent survival rate was similar for birds that used sheltered sites infrequently (natal dispersal of juveniles in autumn; Fig. 4; $\Phi = 0.986$; 95% CrI = 0.975–0.994) and those that used them regularly (adults and juveniles in summer, juveniles in winter; Fig. 4; $\Phi = 0.986$; 95% CrI = 0.978–0.992), but was substantially higher for birds that frequently used sheltered sites (adults in autumn and winter; Fig. 4; $\Phi = 0.997$; 95% CrI = 0.989–1). Thus, cryptic roosting behaviour was associated with increased survival rates.

Avian predation is assumed to occur mainly during daytime when little owls are roosting, whereas mammalian predation might occur more often during the night. Avian predation wasgreatest for birds that used sheltered sites infrequently (8.9%, $n = 56$ individuals; 95% confidence interval (CI) = 3–20%), intermediate for birds that used them regularly (4.7%, $n = 128$ individuals; 95% CI = 2–10%), and virtually absent for birds that used them frequently (0%, $n = 38$ individuals; 95% CI = 0–9%). The cause of mortality was avian predation more often in birds that used sheltered sites infrequently (63%) than in birds that used them regularly (50%). Thus, the use of sheltered sites tended to be associated with lower avian predation rates.

Discussion

Roost site selection is thought to be a state-dependent process, affected by costs and benefits related to the current enivronmental conditions and to the intrinsic factors of the bird (Sunde *et al.* 2003). This study suggests that cost–benefit functions of roost site use change with temperature and season, a conclusion supported by other studies showing seasonal changes in roost site use. For example, tawny owls (*Strix aluco*) and Eastern screech-owls (*Megascops asio*) change roosts from exposed sites in tree crowns in the summer to tree cavities during the winter (Merson *et al.* 1983; Smith *et al.* 1987; Belthoff & Ritchison 1990; Sunde *et al.* 2003). Our study was not designed to disentangle the different mechanisms that make exposed roosting disadvantageous across seasons. However, the results provide important correlative insights into this question. The increasing use of sheltered roost sites from summer to winter can have two mutually non-exclusive causes. First, diurnal cryptic behaviour might be important as a protection from predators or mobbing by other birds (Sunde *et al.* 2003). The decreasing camouflage of open roost sites due to lack of foliage in autumn and winter also results in a significant reduction of cryptic roost sites, leaving caves and cavities in trees or anthropogenic structures to provide protection. Secondly, sheltered roost sites may offer thermoregulatory benefits at low temperatures because temperatures might be higher in roost sites than outside. As we do not have data on mobbing, we cannot evaluate the potential costs of this behaviour. However, Sunde *et al.* (2003) suggested that mobbing by other birds might not be an important reason for cryptic roosting behaviour of tawny owls. On the other hand, changing roosts to more exposed sites in summer may have benefits (see Sunde *et al.* 2003). For example, little owls regularly hunt during the day, in particular in the breeding season and summer months when the nights are short (van Nieuwenhuyse *et al.* 2008). Consequently, roosting in caves and cavities may impair energy intake by daytime foraging because roosting at sheltered sites hampers roosting and hunting at the same place. Alternatively, more efficient brood guarding from exposed roost sites might explain adult use of more open roost sites in the dependent period of young in summer. However, to investigate the effect of brood guarding on roosting behaviour, comparative data on the summer roost sites of non-breeding adults would be required.

We found an effect of temperature on roost site selection. Exposed open sites in tree canopies were selected when conditions were warmer, whereas multi-entrance cavities and wood stacks were increasingly used at low temperatures. It is likely therefore that sheltered sites provide thermoregulatory benefits at low temperatures. This is in line with studies showing higher winter temperatures within than outside cavities (McCafferty *et al.* 2001; Wiebe 2001; Coombs *et al.* 2010; Grüebler *et al.* 2013). In addition to the effect of temperature, we found an effect of season on roost site selection. Little owls increased their use of sheltered sites from summer to winter, suggesting that increased use of sheltered roost sites in winter might also be driven by other factors. First, wind could affect roosting behaviour, as sheltered sites also provide protection from increased thermal conductance due to wind (Bakken 1990; Bakken 1991; Wiersma & Piersma 1994), and the effect of thermal conductance on thermoregulation is expected to be higher at low than at high temperatures. Moreover, our results show that individuals in life-history stages frequently using sheltered roost sites experienced lower mortality than individuals in life-history stages frequently roosting at open sites. Thus, we suggest that predator avoidance might be an important fitness-related factor affecting roosting behaviour, resulting in more cryptic roost sites in winter when protective foliage is missing. This is corroborated by the fact that the main cause of mortality in little owls in our study area is predation (more than 70% of dead radio-tagged birds died from predation; own unpubl. data). Furthermore, the preference for multi-entrance cavities over single-entrance cavities accords with predator avoidance strategies (Tomé *et al.* 2004).

In summer, adult and juvenile little owls showed marginal differences in roost site selection, but this was not the case after juveniles left the natal home-range in autumn.

Juveniles used significantly less sheltered sites during natal dispersal than before, and even in winter home-ranges the use of sheltered sites was significantly lower than in adults. This is one of the first studies showing that roosting behaviour differs between life-history stages, in particular between age classes and during natal dispersal (but see Sunde *et al.* 2003). These roosting patterns have two potential explanations. First, dispersal and wintering habitats might hold few or no sheltered roost sites, leading to a reduced use of these resources simply due to limited availability. This is probably the case for nestboxes. Thus, juvenile little owls use fewer nestboxes after leaving the natal home-range simply because they often occupy habitats without boxes. This may happen because they are excluded by territory owners from occupied high-quality habitats with nestboxes. Secondly, juvenile little owls are likely to have limited knowledge of the availability and quality of sheltered sites in their current short-term habitat. They need to become familiar with the new area first (Delgado *et al.* 2009) and may use open sites partly to gain information. Thus, familiarity with the home-range might be an important component of little owl winter ecology. In conclusion, our results suggest that the costs of natal dispersal could include increased predation threat and higher energy expenditure for thermoregulation.

CONSERVATION IMPLICATIONS

This study shows that adequate roost sites are probably an important habitat requirement for little owls and that the overall habitat quality of an area is likely to incorporate the availability of this resource. In particular, preferred large tree cavities with multiple entrances may increase the quality of agricultural habitats through multiple fitness advantages promoted by reduced predation risk and improved thermoregulation. Thus, habitats providing adequate food supplies and foraging structures might be unsuitable year-round habitats if suitable roost sites are lacking. We propose that maintenance of existing cavities and promotion of new ones be incorporated in agricultural landscape management plans targeting little owls. In particular, providing nestboxes may be a valuable measure to increase habitat quality for little owls. A pilot study confirms that little owls accept artificial roost sites mounted on fruit trees in occupied home-ranges (own unpubl. data). However, it remains unknown whether habitats without any adequate natural roost sites can be enhanced to become breeding habitats exclusively by providing artificial roost sites.

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Table 1. Number of little owl roost sites and number of individuals (in parentheses) located during the different time periods of the year 2010.

	Summer	Fall	Winter	Total
Adults	140 (24)	123 (20)	55 (19)	318 (24)
Juveniles	435 (75)	352 (60)	118 (44)	905 (75)
Total	575 (99)	475 (80)	173 (63)	1223 (99)

Table 2. Rate of use of sheltered roost sites (without considering open roost sites) by adult and juvenile little owls across seasons. Number of locations and confidence intervals are given in parentheses.

	Adults			Juveniles		
Sheltered site	Summer	Autumn	Winter	Summer	Autumn	Winter
Tree cavities	0.42 (*n* = 33) (0.31-0.53)	0.48 (*n* = 48) (0.38-0.58)	0.51 (*n* = 25) (0.36-0.66)	0.49 (*n* = 124) (0.43-0.55)	0.49 (*n* = 81) (0.42-0.57)	0.68 (*n* = 47) (0.56-0.79)
Nestboxes	0.34 (*n* = 27) (0.24-0.46)	0.40 (*n* = 40) (0.30-0.50)	0.35 (*n* = 17) (0.22-0.50)	0.31 (*n* = 79) (0.26-0.37)	0.21 (*n* = 34) (0.15-0.28)	0.09 (*n* = 6) (0.03-0.18)
Stacks of wood	0.23 (*n* = 18) (0.14-0.34)	0.12 (*n* = 12) (0.06-0.20)	0.14 (*n* = 7) (0.06-0.27)	0.17 (*n* = 44) (0.13-0.23)	0.22 (*n* = 36) (0.16-0.29)	0.12 (*n* = 8) (0.05-0.22)
Buildings	0.01 (*n* = 1) (0.00-0.07)	0.01 (*n* = 1) (0.00-0.05)	0.00 (*n* = 0) (0.00-0.00)	0.02 (*n* = 6) (0.01-0.05)	0.08 (*n* = 13) (0.04-0.13)	0.12 (*n* = 8) (0.05-0.22)

Table 3. Results of the generalized linear mixed model analysing the factors affecting the use of sheltered roost sites. Reference values (age: adults; season: autumn) were set to zero.

	Estimate	SE	LR-Value	*P*
Intercept	1.99	0.34	--	--
Age	-1.95	0.34	12.61	<0.001
Temperature	-0.03	0.01	5.00	0.025
Precipitation	-0.02	0.01	1.62	0.203
Season	--	--	13.98	<0.001
Summer	-1.39	0.33	--	--
Winter	0.66	0.54	--	--
Age x Season	--	--	40.74	<0.001
Summer	2.13	0.36	--	--
Winter	0.16	0.59	--	--

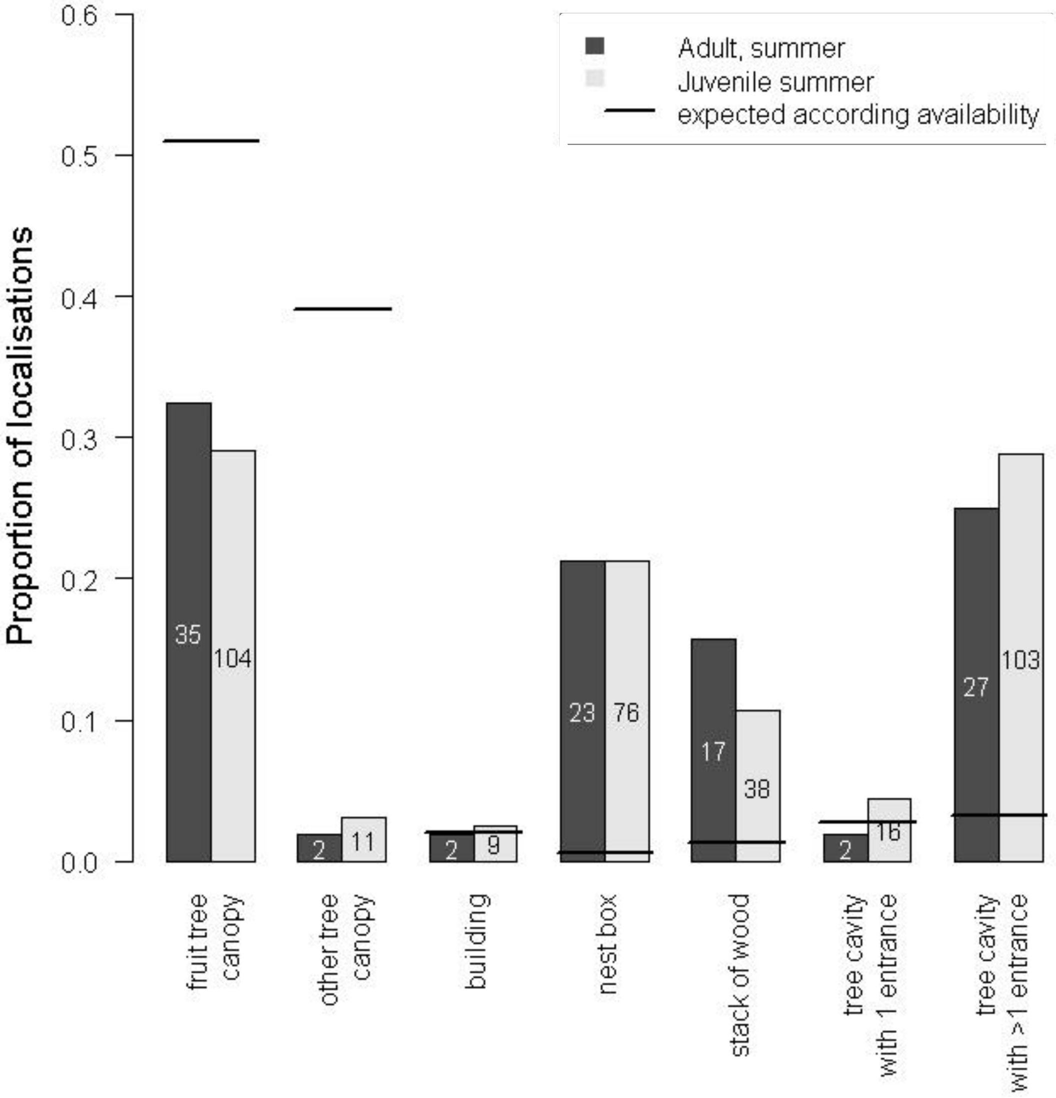

Fig. 1. Proportion of roost sites used by adult (darker bars) and juvenile (lighter bars) little owls in the summer period before juveniles leave the natal home-range. Black lines within and above bars indicate the available proportion of roost sites (i.e. the expected rate if used according to availability). Numbers within bars indicate number of locations.

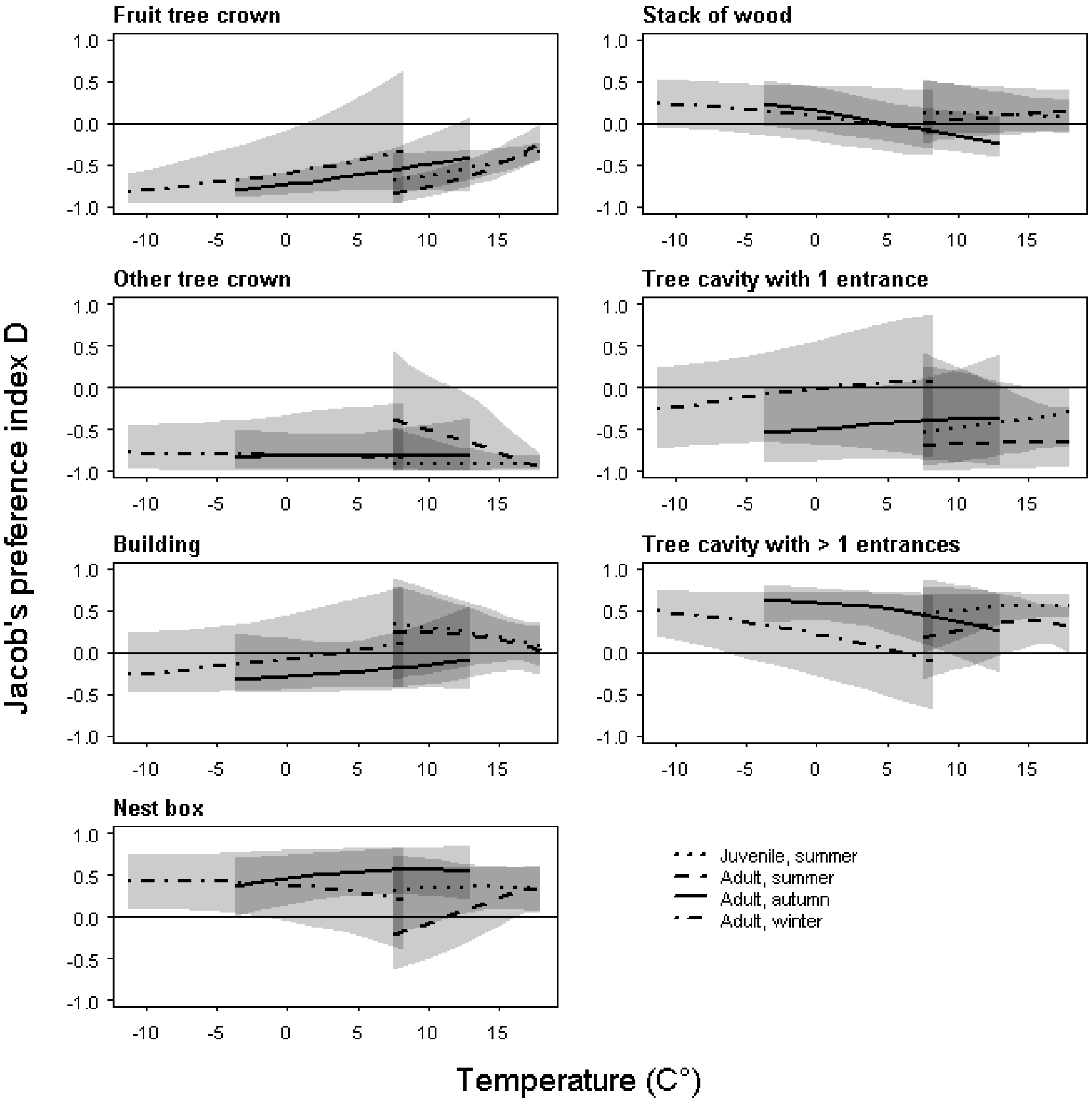

Fig. 2. Jacobs' preference index for different roost site types in relation to ambient temperature and age in different time periods (juveniles summer = dotted lines; adults summer = dashed line; adults autumn = solid line; adults winter = dot-dashed line). Grey areas show 95% CrI for the groups. Credible intervals above zero represent a significant over-proportional use of roost sites, whereas credible intervals below zero show a significant under-proportional use of roost sites. Parameter estimates (and se) of roost site use from the multinomial logistic regression model, the basis for the derivation of Jacobs' preference indices, are given in Table S1. For juvenile birds in autumn and winter, no preference indices could be calculated because the roost site availability remains unknown during natal dispersal and within wintering habitats.

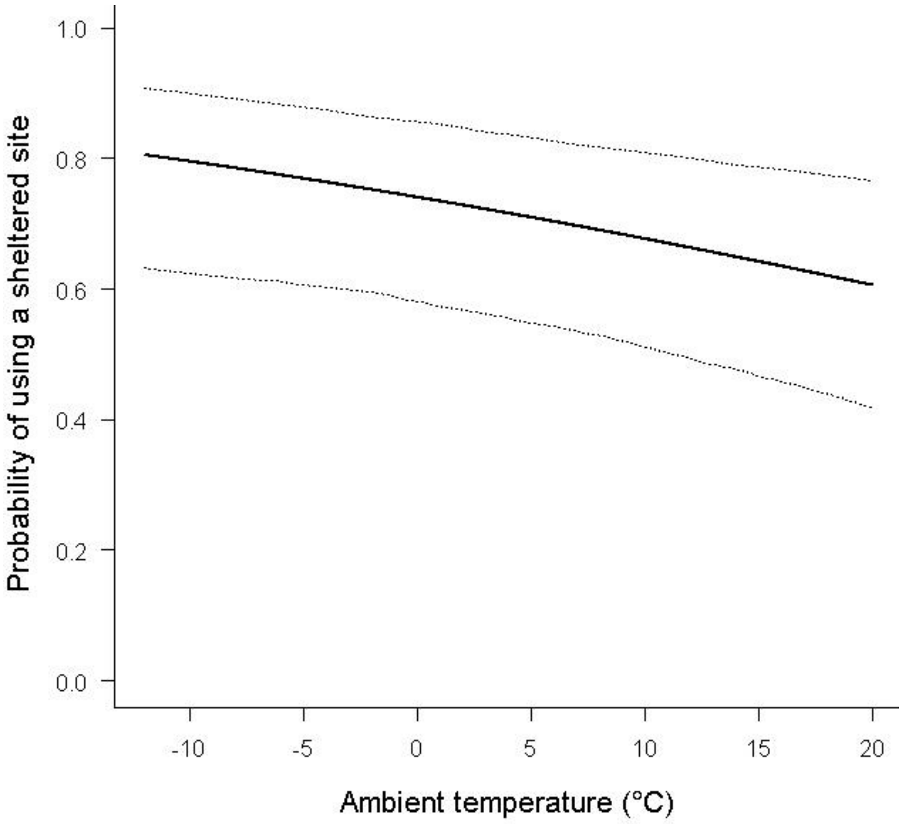

Fig. 3. Predicted values (generalized linear mixed models with binomial error distribution) of roost site use by little owls in relation to ambient temperature. Dotted lines indicate 95% CrI.

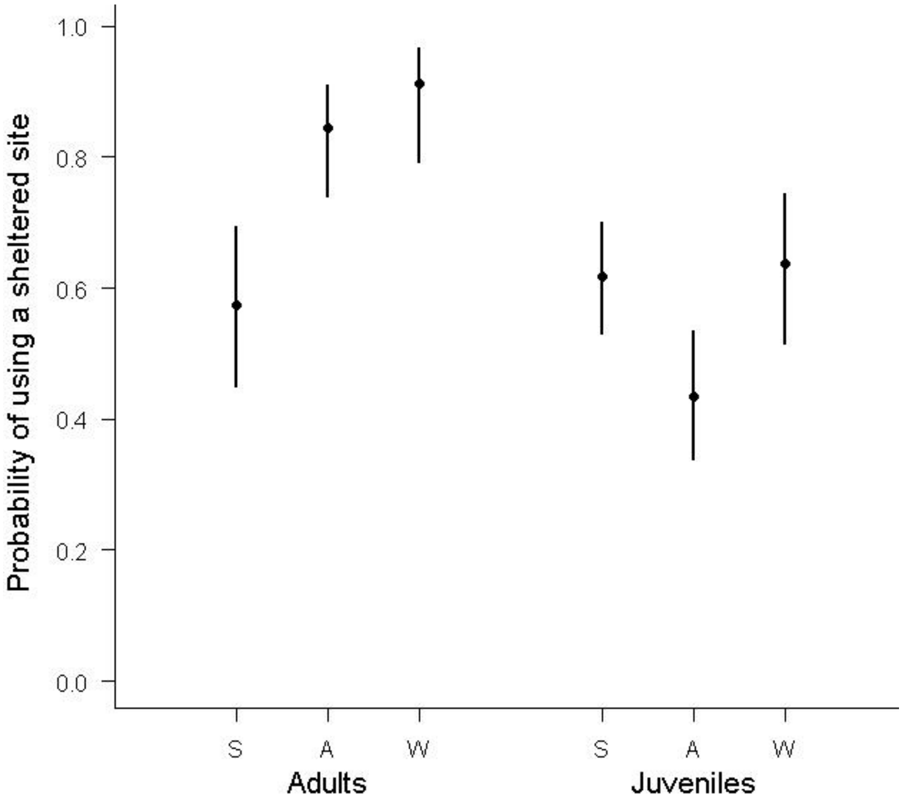

Fig. 4. Predicted values (generalized linear mixed models with binomial error distribution) of roost site use by little owls in relation to age and season (S = summer; A = autumn; W = winter), irrespective of the effect of temperature. Error bars indicate 95% CrI.

Supporting information

Table S1. Parameter estimates (± se) of the multinomial logistic regression model. "Building" was the reference category for which all parameters were fixed to zero. Parameters significantly different from zero are marked with asterisks.

	fruit tree crown	nestbox	other tree crown	stack of wood	tree cavity with >1 entrance	tree cavity with 1 entrance
Intercept	2.88* ± 0.66	0.80 ± 1.11	-1.47 ± 1.15	-2.84* ± 1.31	2.62* ± 0.69	-0.32 ± 0.98
Temperature	1.02 ± 0.82	0.44 ± 0.88	0.98 ± 1.04	0.37 ± 0.95	0.58 ± 0.85	0.96 ± 1.01
adult, fall	1.20 ±1.42	2.77* ± 1.38	2.73 ± 1.50	-0.51 ± 1.83	1.29 ± 1.43	1.42 ± 1.82
adult, summer	-0.13 ± 1.05	0.05 ± 1.18	-0.67 ± 1.66	0.63 ± 1.47	-0.23 ± 1.06	-1.48 ± 1.48
adult, winter	0.01 ± 2.22	0.78 ± 1.94	0.99 ± 2.30	-0.20 ± 2.24	-0.70 ± 1.89	2.09 ± 1.91
adult, fall x temperature	-1.15 ± 1.46	-1.18 ± 1.43	-1.86 ± 1.61	-3.04* ± 1.32	-2.01 ± 1.41	-1.65 ± 1.65
adult, summer x temperature	1.56 ± 1.54	1.28 ± 1.64	-2.12 ± 1.98	1.23 ± 1.77	0.35 ± 1.56	0.38 ± 2.08
adult, winter x temperature	-1.05 ± 1.59	-1.95 ± 1.34	-2.64 ± 1.42	-2.71 ± 1.36	-2.53 ± 1.28	-1.68 ± 1.55

CHAPTER 5

Onset of natal dispersal in little owls (*Athene noctua*) in relation to nestling food supply and timing of breeding: Evidence from a field experiment

Marco Perrig, Martin U. Grüebler, Herbert Keil & Beat Naef-Daenzer

To be submitted

Abstract

Dispersal is an individual-based process with profound effects on the dynamics, persistence and expansion of populations. An individual's decision when to depart is an integral part of the dispersal process, likely bearing consequences for the following stages of dispersal (i.e. transience and settlement). Thus, knowing which factors affect the onset of dispersal is essential to understand the ontogenetic and ecological mechanisms and the causes and functions of natal dispersal. Intrinsic, ontogenetic and environmental factors may influence the onset of dispersal. In addition, fitness-relevant consequences of variation in timing of the onset of dispersal may exist for both parents and juveniles. However, empirical and experimental evidence is scarce. To identify factors affecting the onset of dispersal in little owls (*Athene noctua*), we conducted a partial cross-fostering and food supplementation experiment. The onset of dispersal (defined as the first exploration beyond the natal home-range) was determined in 144 radio-tracked juveniles. The onset of natal dispersal in little owls was primarily determined by the foster environment. The original environment had no significant effect on the onset of dispersal. Furthermore, food supplementation during growth had neither a direct effect on the onset of dispersal, nor through the fledgling's physical traits. The onset of dispersal in little owls peaked in mid-August, irrespective of the hatching date. Juveniles did not explore beyond the natal home-range immediately upon reaching independence at an age of c. 70 days. Instead, juveniles prolonged their time in the parental home-range by up to 50 days (depending on the hatching date). This suggests that owlets benefit from increasing the time in the parental home-range compared to potential benefits from dispersing early. Except the lower threshold age the onset of dispersal in little owls appears not to be ontogenetically determined. Instead, changes in parent-offspring behaviour or seasonal changes in the environment may drive the timing of the onset of dispersal.

Keywords

Timing of departure, ontogenetic factors, environmental factors, carry-over effects, food supply during growth.

Introduction

Dispersal is an important process within the life-history of all forms of life. In actively dispersing species, it is an individual behavioural strategy, which has profound effects on the dynamics, persistence and expansion of populations (Clobert *et al.* 2001). Thus, dispersal links the individual and the population level. In an evolutionary context, dispersal is both subject to selection and a fundamental mechanism maintaining genetic diversity within and between populations (Clobert *et al.* 2001; Clobert *et al.* 2012). As such, understanding dispersal is of paramount importance to understand the spatial dynamics of species distributions within a dynamic environment. However, due to difficulties of tracking individuals during the dispersal stage, the mechanisms and functions behind dispersal are still little understood.

An individual's decision when to disperse is an integral part of the dispersal process (Clobert *et al.* 2001; Bowler & Benton 2005). It may have consequences for the following stages of dispersal (i.e. transience and settlement) and in turn on the life-history stages thereafter (Benard & McCauley 2008). For altricial birds, the general concept of life-history ecology predicts two major trade-offs affecting the timing of departure for natal dispersal. First, for juveniles, early departure is predicted to be advantageous for securing vacant resources (Emlen 1994; Hatchwell & Komdeur 2000), thus improving an individual's prospective fitness (the "early disperser" hypothesis). On the other hand, delayed departure is predicted to increase the benefits of living in the natal home-range (e.g. longer time to build-up energy stores and develop essential skills in the supposed relative safety of the parental home-range). Thus, individuals delaying departure may be better equipped for future challenges than individuals departing early (the "skilled disperser" hypothesis; Ekman 2006; Covas & Griesser 2007). As a consequence, the resulting trade-off between the benefits of early and delayed departure is probably an important determinant of the timing of natal dispersal. Second, particularly in territorial species, the timing of departure may also be influenced by the parent-offspring conflict over the duration of parental care (Sunde 2008; Vergara *et al.* 2010). Parents may promote departure of their young by terminating post-fledging care or by actively chasing them out of their territories. The timing of such parent-induced departure will depend on the trade-off between parental benefits from investing into current or future reproduction. In addition to these trade-offs a range of other factors may modulate the timing of departure (e.g. intrinsic, ontogenetic and environmental factors; Clobert *et al.* 2001). Knowing which factors affect the timing of departure is essential to understand the ecological and evolutionary processes behind the departure decision and natal dispersal. However, only few of these potential factors have been identified through empirical or experimental evidence (e.g. Kennedy & Ward 2003).

Factors influencing departure may carry over from any time period prior to departure (i.e. before hatching or during the nestling or post-fledging stage; Bowler & Benton 2005; Benard & McCauley 2008; Penteriani & Delgado 2011), or act during the departure process itself (e.g. during pre-departure explorations). Identifying time periods which strongly influence the timing of departure is an important first step for understanding the processes behind the departure decision. However, the relative importance of different time periods in influencing the departure decision has barely been determined.

Food is an important ecological factor throughout the entire life of an individual. It influences phenotypic development, everyday activities and reproductive performance (e.g. Martin 1987; Olsson *et al.* 2006; Perrig *et al.* 2014). Food supply is particularly important during growth when individual characteristics develop (Lindström 1999). In turn, these individual traits are likely to affect the decision to leave the natal home-range (Benard & McCauley 2008), but the effects of nestling food supply on the onset of dispersal are poorly studied.

In this study we identified factors determining the onset of natal dispersal in the little owl (*Athene noctua*). Specifically, we investigated three aspects. First, we determined the relative importance of two time periods of juvenile development in affecting the onset of dispersal. Second, we investigated if food supply during growth influences the onset of dispersal. We hypothesized that the onset of dispersal varies in relation to nestling food supply. Third, we analysed the timing of the onset of dispersal in relation to age and hatching date.

We conducted a partial cross-fostering experiment to determine to which extent the onset of dispersal was influenced by 'early factors' (i.e. factors acting prior to the exchange) or 'late factors' (i.e. factors acting after the exchange). We combined the partial cross-fostering experiment with experimental food supplementation during the late nestling and early post-fledging stage (i.e. after the exchange) to determine the effect of food supply during growth on the departure decision. Furthermore, we used hatching date, age and date of first exploration and environmental parameters to analyse whether the onset of dispersal was determined ontogenetically, seasonally, or by environmental factors. If the onset of dispersal is mainly ontogenetically determined, individuals are expected to disperse at the same age, irrespective of their hatching date (i.e. a positive correlation between hatching and departure date). If the onset of dispersal is related to seasonal changes, individuals are expected to start dispersal in the same period, irrespective of their age (i.e. a negative correlation between hatching date and the age at departure). Furthermore, we included characteristics of the parental home-ranges and brood size as potential factors affecting the onset of dispersal.

Materials and methods

STUDY SPECIES AND STUDY AREA

The little owl is a territorial species with obligate natal dispersal. Juvenile little owls in central and northern Europe typically hatch in May and fledge at c. 30 days of age (van Nieuwenhuyse *et al.* 2008). After fledging, juvenile little owls stay for several weeks within the parental home-range and regularly return to the nest (Pedersen *et al.* 2013). Dispersal typically starts with short exploration trips (Eick 2003) before individuals depart from their natal home-range during September and October (Pedersen *et al.* 2013). Ring recoveries suggest that females disperse farther than males (van Nieuwenhuyse *et al.* 2008). Little owls usually reproduce for the first time at an age of one year (van Nieuwenhuyse *et al.* 2008).

This study was conducted in a population of about 220 little owl breeding pairs in Southern Germany (Landkreis Ludwigsburg, Baden-Württemberg, 48°53′43″N, 9°11′45″E). Virtually all pairs of this population breed in nestboxes. From 2009 to 2011, 93 broods were monitored from late incubation onwards using regular brood controls, camera traps and radio-telemetry. One brood with three chicks hatched exceptionally late in the season (i.e. 20 days later than any other individual in this study, Fig. 1) and was excluded from the analysis. A total of 144 juveniles from 67 broods departed from their home-ranges and thus, were included in the analysis.

EXPERIMENTAL DESIGN

In the partial cross-fostering field experiment, two synchronous broods were denoted as partner broods. Depending on brood size, one or two nestlings of similar age and body weight were exchanged among partner broods, keeping brood sizes constant. Exchanges were carried out at c. 14 days of age. One of the two partner broods was randomly assigned to experimental food supplementation. Food supplementation started after the exchange. Every second day for 36 days, experimental broods were provided with extra food. A total of 480 g of dead laboratory mice per nestling was deposited inside the nestbox of supplemented broods, 20 g per visit and nestling for the first six visits, 30 g per visit and nestling thereafter. Thus, food supplementation continued until juveniles were c. 50 days old (i.e. three weeks after fledging). Supplemented food represented a c. 40% increase compared with natural food supply (Juillard 1984). Control broods were treated equally (i.e. regularly visited) except that no food was supplied.

Partial cross-fostering and food supplementation were conducted in 2010 and 2011. To improve the power of the analysis, additional broods for which no synchronous partner brood was available were also included. Accordingly, none of the additional broods were cross-fostered, but a part was food supplemented. All additional broods were treated according to the same protocol (i.e. regularly visited, measured, radio-tagged). No treatment was performed in 2009. Overall, 62 of the 144 individuals considered in this study were food supplemented and 52 were exchanged (Table 1).

DATA COLLECTION

Individual traits

The hatching date of each nestling was determined using developmental illustrations (van Nieuwenhuyse *et al.* 2008) and the equations given in Juillard (1979). Feather samples were obtained for genetic sex determination of the nestlings. Individual characteristics at fledging may affect the onset of dispersal. They may represent heritable quality or indirect effects of environmental factors during growth (e.g. nestling food supply). Thus, prior to fledging (at the age of 28.7 days ± 2.93; mean ± 1 SD, $n = 239$), six individual traits were measured: body mass (to the nearest 0.1 g), the presence or absence of subcutaneous fat deposits under the wing, tarsus length (to the nearest 0.1 mm), wing length (to the nearest 0.5 mm), countenance (i.e. struggling during handling or not) and eye coloration (i.e. intense or pale). In 2009, only body mass and tarsus length were measured. For details see Perrig *et al.* (2014).

In addition, body mass, wing length and tarsus length were measured several times during the nestling stage (for details see Perrig *et al.* 2014). Here, we used the measurements closest to fledging. Because these measures are age dependent, residuals of these measurements on the fitted growth curves through all data points (TableCurve 2D Version 5.01, Systat Software Inc., Erkrath, Germany) were used for the analysis.

Habitat-related variables

The onset of dispersal may depend on the quality of the habitat in which an individual grows up, including food availability, conspecific density and predation risk (Lambin *et al.* 2001; Weisser *et al.* 2001; Benard & McCauley 2008). Accordingly, three variables reflecting different aspects of habitat quality were recorded for each nestbox. First, the dominant habitat type (i.e. orchard dominated or dominated by agricultural land) reflects structural diversity and food availability (Apolloni 2013; Scherler 2014). Second, brood size at fledging may represent overall habitat quality and local environmental conditions during the breeding period. And third, the distance from the nestbox to the nearest forest edge is a habitat characteristic indicating the proximity to unsuitable little owl habitat (van Nieuwenhuyse *et al.* 2008; own unpubl. data).

Radio-telemetry

Prior to fledging, all chicks were tagged with VHF radio-transmitters of own construction (Naef-Daenzer *et al.* 2005). Tags were mounted with a back-pack figure-8-harness (Kenward 2001). Life expectancy of the tags was c. 400 days and the range with handheld 3-element Yagi antennas was up to 40 km. The total tag weight (including harness) was c. 7 g. This is

4.5% of the mean body mass of adults captured during our study (i.e. less than the maximum of 5% recommended in Caccamise & Hedin 1985; Kenward 2001; Jackson *et al.* 2011). We located all individuals at least three times per week using the homing-in technique (Kenward 2001). This allowed to record the position and to detect whether birds were still alive. During the main dispersal stage in September and October (van Nieuwenhuyse *et al.* 2008), tracking was intensified to 4-5 re-locations per week.

ANALYSIS

Pre-departure explorations are part of the dispersal process (Matthysen *et al.* 2010; Debeffe *et al.* 2013). Thus, we defined the onset of dispersal as the time of an individual's first exploration outside of the natal home-range (Fig. 2). The natal home-range was defined as the area within 300m around the nestbox.

Factors affecting the onset of dispersal were analysed using linear mixed effects models with the package arm (Gelman & Su 2013) in the statistical software R 3.0.2 64-bit (R Core Team 2013). For all models, residuals were inspected to confirm model assumptions. Ninety-five per cent credible intervals (CrI) for all fixed and random factors were obtained from the simulated posterior distribution (5000 simulations).

The effect of food supply during growth on the onset of dispersal was modelled as a function of experimental food supplementation, sex, year and hatching date. The original family (i.e. the family before the exchange) and the foster family (i.e. the family after the exchange) were included as random factors. This allowed estimating the relative importance of early factors (i.e. before the exchange) and late factors (i.e. after the exchange) for the onset of dispersal. Large variance between foster families compared to the variance between original families (Fig. 3a) indicates that the onset of dispersal is more similar between foster siblings than between original (i.e. genetic) siblings. Similarly, a large variance between original families indicates that factors from the original environment are more important (Fig.

3b). Furthermore, the family factors accounted for individual dependencies within family units. Because the patterns of age and date at the onset of dispersal reveal if the onset of dispersal is ontogenetically determined or seasonally timed, the analysis was run for both, age and date at the onset of dispersal as the dependent variable.

Individual traits and environmental factors

To assess other factors potentially affecting the age at the onset of dispersal, six individual traits (i.e. body mass, fat deposits, tarsus length, wing length, countenance and eye coloration) and three habitat-related factors (i.e. habitat type, brood size and the distance to forest) were added to the model described above. Furthermore, a quadratic term for the distance to forest was also included, since we expected the effect to diminish at large distances to the forest. Because in 16 individuals some traits were not measured, this analysis was conducted on a reduced dataset.

Results

EXPERIMENTAL EFFECTS ON THE ONSET OF DISPERSAL

The factors acting after the exchange were significantly more important in determining the onset of dispersal than factors acting before the exchange. The onset of dispersal varied considerably more among foster families than among original families ($\mathrm{var}_{\mathrm{Foster}} = 56.95$; $\mathrm{var}_{\mathrm{Original}} = 18.71$; Table 2, Fig. 3). The ratio between the variances of the two random factors (i.e. $\mathrm{var}_{\mathrm{Foster}} / \mathrm{var}_{\mathrm{Original}}$) for all 5000 simulated parameter sets confirmed this: all ratios were larger than 1.85 ($P < 0.0002$). In addition, according to Akaike’s Information Criterion (AIC; Burnham & Anderson 2002) only the random factor ‘foster family’ had a considerable effect on the onset of dispersal: Including ‘foster family’ improved the AIC by 3.29 units, whereas including ‘original family’ reduced the AIC support by 0.64 units.

The experimental food supplementation during growth had no direct effect on the onset of dispersal. Supplemented and control juveniles first left their natal home-range at similar ages (accounting for hatching date, sex, year and familial relationships or when adding other factors to the model; Tables 2a & 3) and at similar dates (Table 2b). Furthermore, no indirect effects of food supplementation during growth acting through individual traits on the onset of dispersal were detected. None of the fledgling traits which are affected by nestling food supply (i.e. body mass, fat deposit, wing length, countenance and eye coloration; Perrig *et al.* 2014) had any considerable effect on the onset of dispersal (Table 3).

AGE AND DATE

Date-related factors were the most important determinants of the onset of dispersal. On the one hand, the later in the season an individual hatched, the younger it started exploring areas beyond the natal home-range (Fig. 4a). The slope of this negative linear relationship was not significantly different from minus one (slope =-0.916, 95% CrI = -1.247 – -0.567, Table 2a). Thus, for each day the hatching date advanced, the age at the onset of dispersal decreased by approximately one day. On the other hand, the hatching date had no effect on the date of the onset of dispersal (slope = 0.084, 95% CrI = -0.263 – 0.430, Table 2b). Juvenile little owls first left their natal home-range around mid-August, irrespective of their hatching date (Fig. 4b). As a consequence, individuals hatching early in the season spent more time in the natal home-range before the onset of dispersal than individuals hatching late in the season.

Most individuals first explored beyond the natal home-range at an older age than c. 70 days (Fig. 4a). Thus, in addition to the strong seasonal timing, the data indicate an ontogenetic threshold below which individuals rarely showed exploratory behaviour.

OTHER FACTORS AFFECTING THE ONSET OF DISPERSAL

Tarsus length was the only fledgling trait significantly affecting the onset of dispersal (-1.337, 95% CrI = -2.393 – -0.263, Table 3). Larger fledglings first ventured out of the natal home-range at an earlier age, with a 5 mm difference in tarsus length resulting in a difference of 6.7 days in age at departure (Fig. 5a).

Among the habitat-related variables (i.e. distance to forest, brood size at fledging and habitat type) the distance to the nearest forest edge affected the onset of dispersal in a non-linear manner (Table 3). The onset of dispersal of juveniles having fledged 150 m from the forest edge was on average 11 days earlier than juveniles having fledged 1 km from the forest edge (Fig. 5b). At distances exceeding 1 km, the predicted age at the onset of dispersal declined again, probably as an effect of the quadratic function (Fig. 5b).

Neither sex nor year significantly affected the onset of dispersal (Tables 2 & 3).

Discussion

This study highlights that the onset of natal dispersal in little owls occurred in a characteristic period of the year, irrespective of the hatching date. Most juveniles started venturing beyond the natal home-range around mid-August, although some did so as early as late July. This pattern is consistent with an earlier study on little owls, where non-local (i.e. prospecting or dispersing) juveniles were observed around established territories from July onwards (M. Exo, unpubl. data). The timing of breeding therefore affected the duration of the post-fledging stage (i.e. the time between fledging and the onset of dispersal), rather than the timing of the onset of dispersal. Individuals hatching early in the season spent substantially more time in the natal home-range than did individuals hatching late in the season. This suggests that breeding early in the season (i.e. juveniles hatching around mid-May) yields benefits in ultimate reproductive output, although nestling survival was considerably better later in the season (Perrig *et al.* 2014).

Juvenile little owls did not start dispersing before c. 70 days of age. At this stage in the ontogeny they become independent (van Nieuwenhuyse *et al.* 2008; Pedersen *et al.* 2013). Although females appear to disperse over larger distances (van Nieuwenhuyse *et al.* 2008) the two sexes did not differ in the age of first explorations out of the parental home-range.

While independence from parental care is a precondition for dispersal, this step in the juveniles' life-history was not the main trigger for pre-dispersal exploratory behaviour. Early hatched owlets stayed within the natal home-range up to an age of c. 120 days, that is, some 50 days after the termination of parental feedings. This result contradicts the general hypothesis that early dispersal is advantageous in the competition for vacant resources. According to this hypothesis, juveniles are expected to disperse quickly upon reaching independence (Emlen 1994; Hatchwell & Komdeur 2000). Instead, juvenile little owls extended the post-fledging stage to an extent depending on the hatching date. Therefore, our results are in line with the general hypothesis that juveniles staying longer in the natal home-range may gain essential skills for later life-history stages (Ekman 2006; Covas & Griesser 2007). However, we have no evidence, whether the duration of the post-fledging stage within the natal home-ranges had an effect on fitness relevant parameters (e.g. survival or reproduction).

The mechanism synchronizing the onset of dispersal around mid-August remains unclear. Although seasonal changes in food availability may occur, no sharp changes in the environment are evident in this period. We hypothesize that various seasonal changes in the social system and related behavioural dynamics may be a main determinant timing the onset of dispersal in juveniles. First, the autumn and winter home-ranges of resident adults are significantly larger than during the reproductive period. The related changes in the parents' spatial behaviour also occur in late summer (own unpubl. data). In parallel, parents may also change their behaviour towards the young. Second, adult little owls begin to moult in early autumn (van Nieuwenhuyse *et al.* 2008), which may also be related with a change in the behaviour towards offspring.

EXPERIMENTAL EFFECTS

Partial cross-fostering revealed that the foster environment (i.e. after the exchange) was more important in timing the onset of dispersal than factors of the original family. The mechanism behind the small effect of the original family may be based on a heritable trait affecting the onset of dispersal. In birds, size is largely genetically determined (e.g. Schuett *et al.* 2013). In turn, large fledglings (in terms of tarsus length) started exploring at a younger age than small individuals. Furthermore, we found no evidence that parental food supply during growth affected the onset of dispersal within the overall peak in August. Experimental food supplementation had no direct or indirect (i.e. through five individual traits) effects on the timing of first explorations. We conclude that young little owls base their decision when to start exploring mainly on current information (e.g. environmental cues, parental behaviour and internal state) rather than on past experiences or conditions.

DISTANCE TO FOREST

Little owls generally avoid forested areas (van Nieuwenhuyse *et al.* 2008). In another part of our radio-tracking study we found that little owls also avoided forest edges, apparently as a response to elevated predator presence (own unpubl. data). The earlier onset of dispersal in close proximity of forests may be interpreted as a response to predation risk. However, the result may also be an artefact due to inappropriate definition of the natal home-ranges. Since areas closer than 150m to the forest edge are strongly avoided (own unpubl. data), home-ranges close to forests are probably shaped asymmetrically around the breeding site. In such cases juveniles may travel more than 300m from the nestbox without leaving the natal home-range.

In conclusion, the results show that the onset of dispersal in little owls occurs in a narrow time window within the year with little between-year variation. Furthermore, the individuals' decision appears not to be influenced by the energy supply during growth. However, the family environment in which a juvenile reaches independence had a marked effect on the onset of dispersal. Also, juveniles growing up in home-range close to forest responded to a potential predation risk by exploring the ranges outside the natal home-range at a younger age. Therefore, the family (as the closest social unit) and coarse-grained habitat features appear to modulate the timing of the onset of dispersal in little owls. Unfortunately, the details of behavioural processes resulting in dispersal are lacking due to the difficulty to observe the birds visually.

The results cannot fully explain the observed pattern in the onset of dispersal. On the one hand, juvenile little owls did not start exploratory behaviour immediately after reaching independence. Thus the "early disperser" hypothesis is not supported. On the other hand, our results partly support the "skilled disperser" hypothesis in that juveniles stay in the natal home-range up to several weeks after reaching independence. However, this fact alone is insufficient for explaining the causes and functions of the observed timing of the onset of dispersal. Both ecological and ethological evidence are required to further explain the observed patterns. As a working hypothesis we suggest that seasonal changes in the physiological state and behaviour of adults terminate parental behaviour in late summer, which may result in intolerant behaviour against offspring.

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Table 1. Distribution of the 144 tagged little owls on the different treatments of the partial cross-fostering and food supplementation experiment.

	Exchanged	Not exchanged	Total
Food supplemented	31	31	62
Control	21	61	82
Total	52	92	144

Table 2. Parameter estimates (and 95% CrI of the posterior distribution) of the models assessing the effects of partial cross-fostering and food supplementation on (a) the age and (b) the date at the onset of dispersal. Significant effects are marked with asterisks. Significances were determined according to the 95% CrI for fixed effects and according to the AIC for random effects (ΔAIC > 2 is considered significant). The variances are given for random effects. The dataset consisted of 144 individuals from 71 original families in 67 foster families.

(a) Modelling the age at the onset of dispersal

Fixed factors	Estimate	95% CrI		
Treatment	0.942	-4.500	6.330	
Hatching date	-0.916*	-1.247	-0.567	
Males	2.210	-1.781	6.162	
2010	0.846	-9.686	11.405	
2011	-1.155	-11.257	8.950	
Intercept	105.519*	92.646	118.027	
Random factors	**Variance**	**95% CrI**		**ΔAIC**
Original family	18.71	10.71	23.51	-0.64
Foster family	56.95*	45.39	92.36	3.29
Residuals	95.62	-	-	-

(b) Modelling the date of the onset of dispersal

Fixed factors	Estimate	95% CrI		
Treatment	0.942	-4.341	6.397	
Hatching date	0.084	-0.263	0.430	
Males	2.210	-1.770	6.052	
2010	0.846	-9.865	11.325	
2011	-1.155	-11.625	8.971	
Intercept	73.519*	60.994	86.296	
Random factors	**Variance**	**95% CrI**		**ΔAIC**
Original family	18.71	10.70	23.42	-0.64
Foster family	56.95*	44.97	92.84	3.29
Residuals	95.62	-	-	-

Table 3. Parameter estimates (and 95% CrI of the posterior distribution) of the model assessing the effects of six individual traits and three habitat-related factors on the age at the onset of departure. Variances are given for random effects. Significant fixed effects according to the 95% CrI are marked with asterisks. The model was based on 128 individuals from 61 original families in 56 foster families.

Fixed factors	Estimate	95% CrI	
Treatment	2.444	-2.809	7.643
Hatching date	-0.949*	-1.310	-0.584
Males	-0.065	-4.423	4.295
2011	1.067	-5.144	7.083
Body mass	-0.087	-0.296	0.115
Tarsus length	-1.337	-2.393	-0.263
Wing length	0.045	-0.328	0.407
Fat deposits	-2.726	-10.002	4.498
Struggling	-0.475	-5.086	4.333
Intense eye coloration	-0.763	-6.199	4.729
Orchard-dominated habitat	-4.530	-9.560	0.695
Brood size	2.319	-0.255	4.897
Distance to forest	0.032*	0.004	0.060
(Distance to forest)^2	-0.000017*	-0.000033	-0.000001
Intercept	91.890*	71.642	112.918
Random factors	**Variance**	**95% CrI**	
Original family	21.36	13.67	30.91
Foster family	20.50	13.20	31.93
Residuals	97.92	-	-

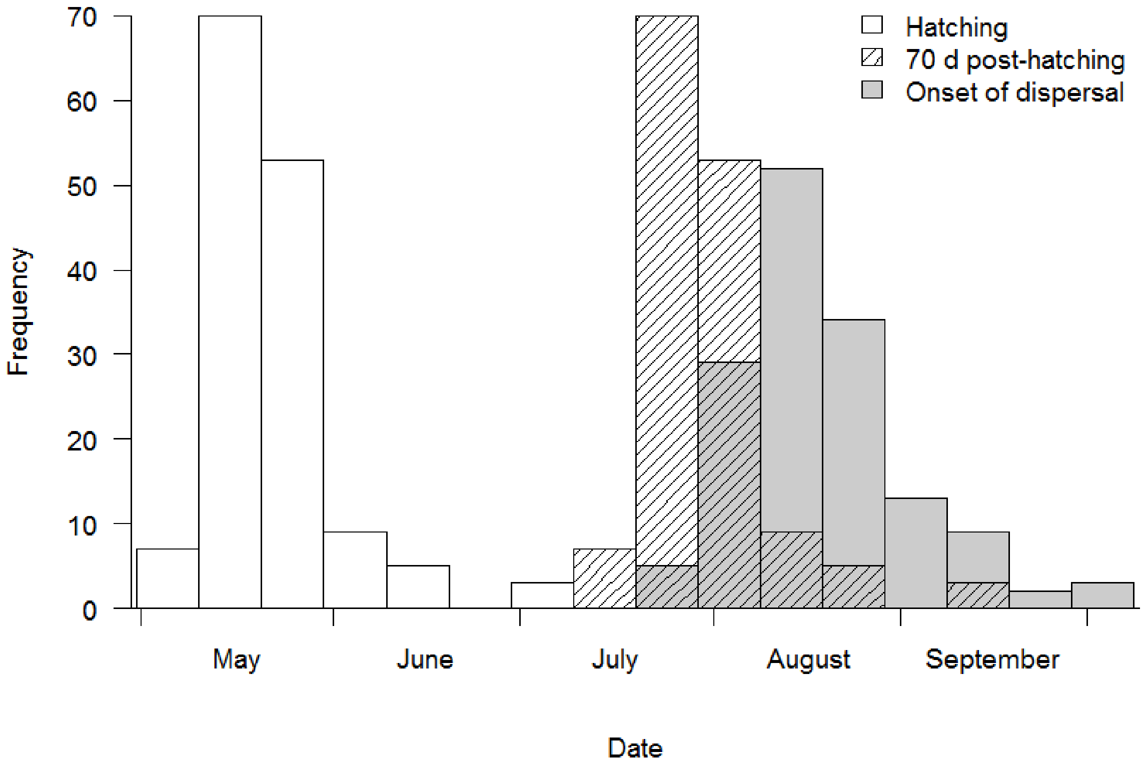

Fig. 1. Histograms of the hatching dates (open bars), the dates when juveniles become independent (i.e. at the age of 70 days; hatched bars) and the onset of dispersal (grey bars) of all 147 tagged little owls that ventured beyond the natal home-range at least once. Most individuals hatched in May and early June. Three siblings hatched in early July. This is considered exceptional for the entire study population over the last 25 years (H. Keil unpubl. data). Thus, these three siblings were excluded from the analysis, resulting in 144 individuals considered in this study.

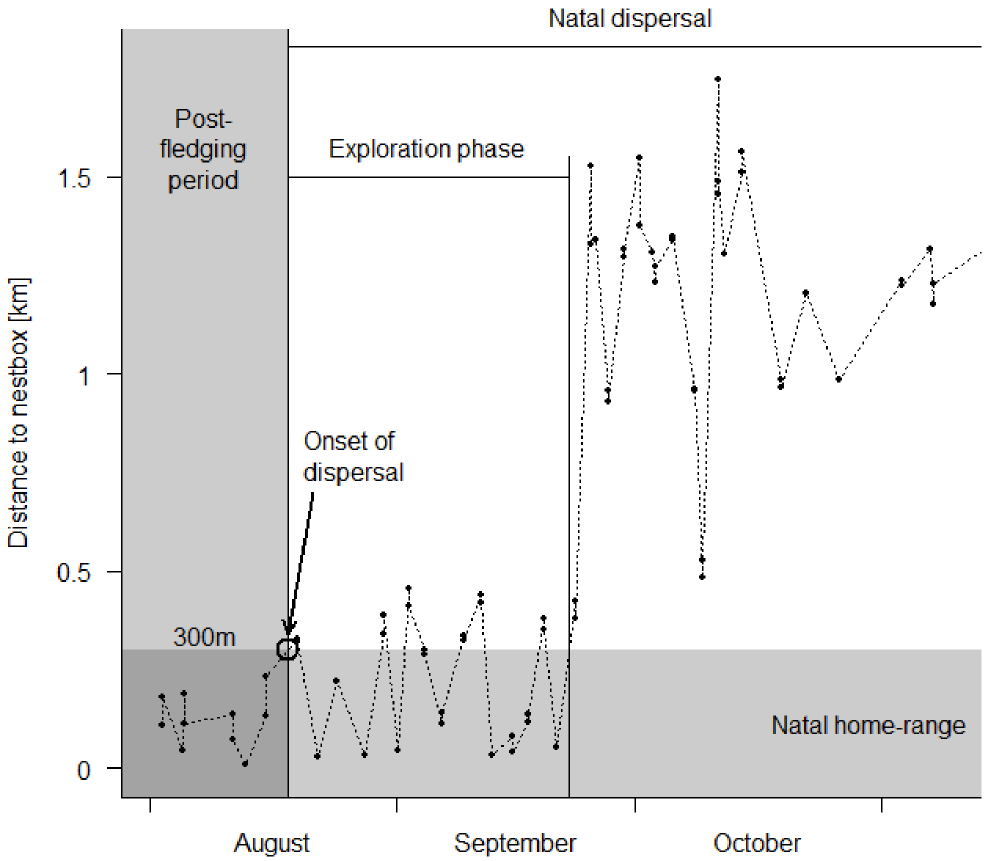

Fig. 2. An example to illustrate how the onset of dispersal was determined. For each known location of an individual (determined with radio-telemetry) the distance to the natal nestbox was plotted against the time (solid circles). The time when the line joining these solid circles crossed for the first time beyond the natal home-range (i.e. 300m from the nestbox, horizontal band shaded in grey) was defined as the onset of dispersal (open circle). The time period before the onset of dispersal was defined as the post-fledging period (i.e. vertical band shaded in grey).

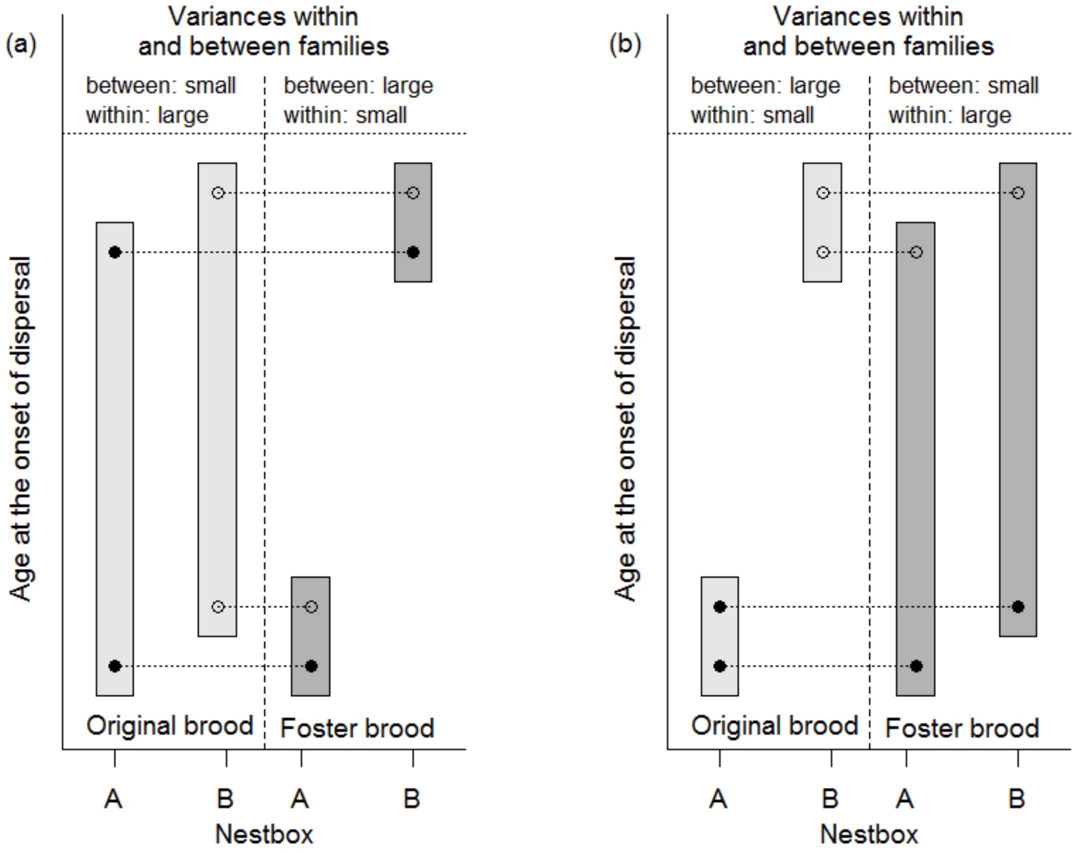

Fig. 3. Schematic representation of the variances between and within families, if (a) factors of the foster family (e.g. habitat quality, local environmental conditions) or (b) factors of the original family (e.g. genetic, maternal and environmental effects) primarily determine the onset of dispersal. If factors of the foster family are important, we expect the onset of dispersal among foster siblings to be more similar than among genetic siblings. Thus, the variance from random factor ‘foster family’ (i.e. the variance between foster families) is expected to be large compared to the random factor ‘original family’. Similarly, if factors of the original family are important, we expect the variance from random factor ‘original family’ to be large. Solid and open circles represent genetic siblings hatched in the nestboxes A and B, respectively. Light and dark grey boxes represent original and foster family units, respectively.

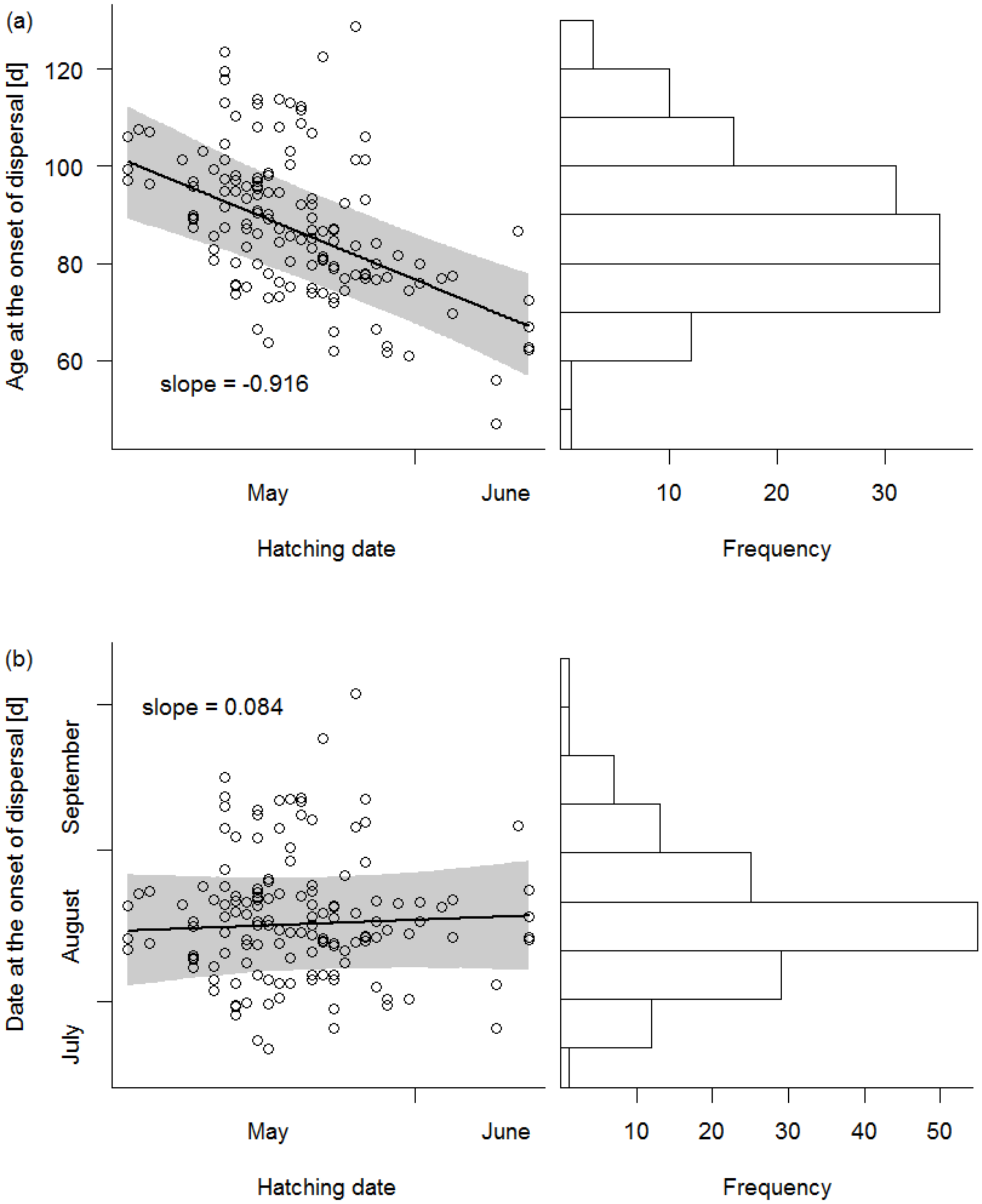

Fig. 4. Patterns of age (a) and date (b) at the onset of dispersal in relation to hatching date. Open circles represent the raw data (*n* = 144). Models controlled for experimental treatment (i.e. food supplementation), sex and year. The solid line represents the prediction for control females in 2009. The 95% CrI from the posterior distribution is shaded in grey. The linear relationships in (a) and (b) were not significantly different from minus one and zero, respectively.

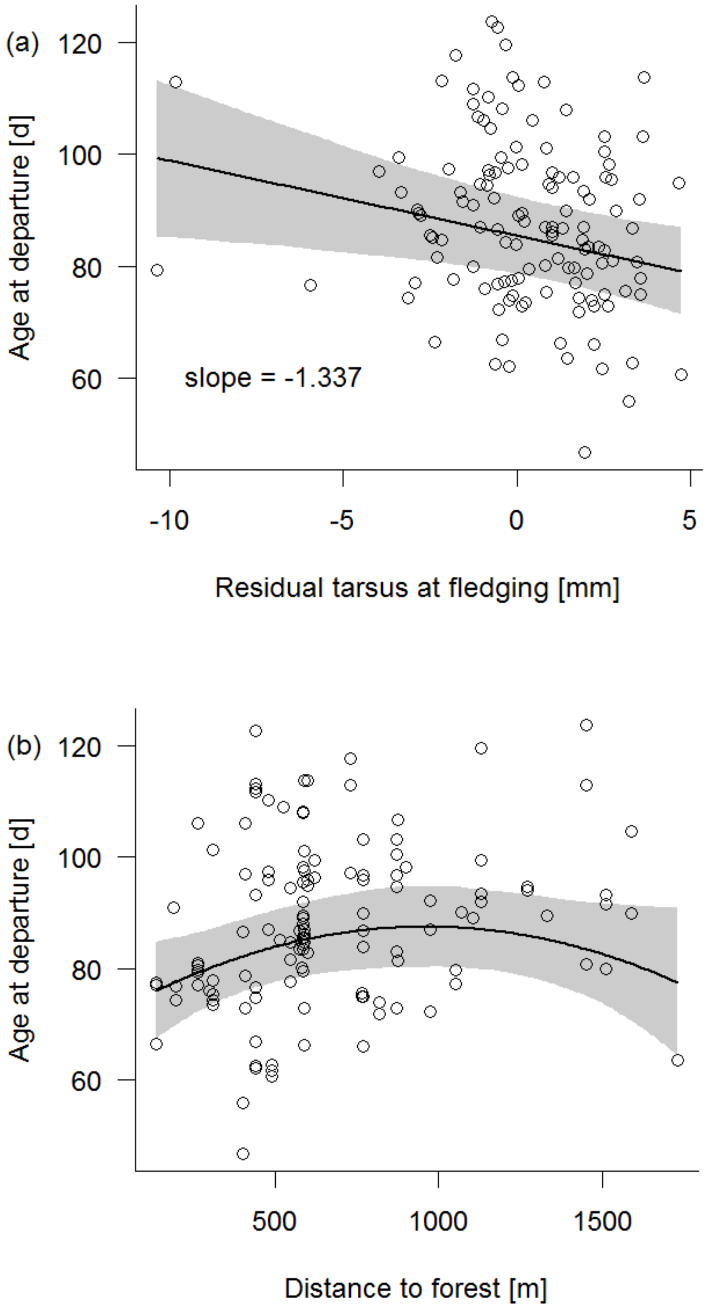

Fig. 5. Effect of the residual tarsus length (a) and the distance from the nestbox to the nearest forest edge (b) on the age at departure. Open circles represent the raw data (*n* = 131). Models included for experimental treatment (i.e. food supplementation), sex, year, six individual traits, and three habitat-related factors. The solid line represents the model predictions for struggling control females from orchard-dominated habitats in 2010 of average size (i.e. body mass, tarsus length and wing length), with fat deposits and intense eye colour. The 95% CrI from the posterior distribution are shaded in grey.

SYNTHESIS

The research field of this thesis is the causal cascade from ecological factors to the physical and behavioural traits of individuals, and further to patterns and processes at the population level. Specifically, I studied the effects of variation in food supply during growth on phenotypic development, on stage-specific survival rates and on the onset of dispersal by combining experimental and analytical approaches. The main conclusion from experimental food supplementation of little owl broods is that local trophic conditions during the nestling and early post-fledging period have a marked impact on the number and physical quality of offspring, and in turn on key demographic parameters such as the number of juveniles that survive to the first reproductive season.

Three major topics are addressed in this thesis. First, I investigated the effects of variation in food supply on juvenile growth and phenotypic traits (Chapter 1). This part gives evidence for bottom-up environmental effects on the productivity and the quality of offspring. Second, I present an analysis of stage-specific survival rates throughout the first year of life (Chapters 2 & 3). This part shows how survival, a key demographic parameter, is linked to trophic conditions, in particular food supply during growth and weather-dependent drops in food availability in winter. As the major proximate cause of mortality was predation, a top-down trophic relationship is an important factor for first-year survival. Third, I investigated two aspects of natal dispersal in little owls: the roosting behaviour during dispersal (Chapter 4) and the characteristics of the onset of dispersal (Chapter 5). The results of this part contradict the general hypothesis that juveniles of territorial species are expected to disperse as soon as they reach independence to increase their chances to secure vacant resources.

THE EFFECTS OF NESTLING FOOD SUPPLY

Experimental food supplementation substantially increased the nestling survival and thus, reproductive success. I conclude that natural variation in food supply to little owl broods will cause similar variation in the productivity of breeding pairs. Furthermore, the variation in food supply affected the phenotypic development in a complex way. Body mass, wing length, fat deposits as well as behavioural traits and eye coloration were affected by nestling food supply. The effects of food supply during growth also carried over into the post-fledging stage (i.e. the period between fledging and the onset of dispersal) through individual traits. Specifically, energy stores accumulated during the nestling period positively influenced survival during the post-fledging stage. These results identify the mechanism how food supply to little owl broods affects reproductive success and, ultimately, the spatial variation in the productivity within a population. I detected no direct or indirect effect of experimental food supplementation on stage-specific survival rates beyond the post-fledging stage. In winter, however, periods of high mortality coincided with periods with a closed snow-cover. Thus, winter survival probably depends on resources within a territory, mainly on the availability of food, and on predation pressure. The experimental food supplementation had no effect on the timing of the onset of dispersal.

SURVIVAL PATTERNS OF THE FIRST YEAR OF LIFE

This thesis also considers survival for each life-history stage in the first year, including an evaluation of the costs of dispersal. Survival rates of seven consecutive periods from hatching to first reproduction were investigated. Thus, the results set the costs of different life-history stages in relation to each other. About half of the first year's mortality occurred before the onset of dispersal, thus in the nestling and the post-fledging stage. During these early stages selection for individual traits occurred. Therefore, the pre-dispersal period is not only important for the quantity but also for the quality of juvenile little owls which leave the parental home-range. Survival rates were relatively low from mid-August to the end of October (i.e. during natal dispersal) and during the winter period. While survival rates within most periods were consistent between years, winter survival was not. This was due to a strong effect of winter conditions on winter survival. Thus, annual variation in individuals surviving the first year of life stems from variable winter conditions. I conclude that in little owls, first year survival is characterized by a cascade of several bottlenecks, differing in the underlying mechanisms. Of these, the dispersal stage represents an important cost in terms of survival.

DISPERSAL BEHAVIOUR

The third theme of the thesis focuses on processes involved in natal dispersal. In particular, I investigated two aspects. First, I investigated a potential behavioural mechanism affecting the mortality during the dispersal period (i.e. in autumn). Little owls used sheltered roosting site less frequently during natal dispersal compared to summer or winter, when little owls were stationary. This suggests that dispersers either used areas with a low availability of cavities or that they did not have enough time to locate sheltered roosting sites in unfamiliar areas during the dispersal process. As a consequence, dispersing little owls were probably more exposed to predation. Additionally, an increased exposure to weather may have increased their energy expenditure while roosting (Stützle 2014). I conclude that the reduced use of sheltered roost sites during dispersal is a contributor towards the considerable mortality in the period of natal dispersal. Second, I determined the main drivers of the onset of dispersal. Juvenile little owls did not leave the natal home-range soon after reaching independence at an age of c. 70 days. This result does not support the hypothesis that juveniles departing early are expected to have advantages in the competition for vacant resources. Instead, individuals often extended their time in the natal home-range by several weeks after reaching independence. This result partly supports the hypothesis that juveniles delaying the stage in the parental home-range may enhance essential skills and thus, gain advantages over juveniles departing early. The factors synchronizing the onset of dispersal around mid-August remain unknown. While no obvious seasonal changes in the environment (e.g. food availability) occur in August, physiological and behavioural changes in adults are evident (e.g. start of the moult, increasing home-ranges). Thus, the synchronous onset of dispersal in little owls is probably linked to some seasonal changes in parental behaviour and related interactions between parents and offspring.

CONCLUSIONS

I draw two main conclusions from this work. First, life-history stages prior to dispersal are crucial for the ecology and population dynamics of little owls. In terms of survival, several bottleneck periods occur in the first year of life of little owls. The most important of these is during the nestling and post-fledging period. The factors affecting survival during these stages are also key factors determining the number of juveniles surviving to first reproduction. The periods of elevated mortality may also increase the probability of selective processes for specific traits. Second, trophic relationships are important drivers of little owl ecology. The marked positive effect of experimental food supplementation during growth on pre-dispersal survival rates highlights that food availability has profound effects on the productivity of little owl populations. Furthermore, effects of experimental food supplementation did not carry over far beyond the end of the treatment. Similarly, the marked effects of short-term reduction in food availability on winter survival indicate that short-term variation in energy supply has immediate consequences for an individual’s survival prospects. Thus, I suggest that little owls are “income survivors” rather than “capital survivors”.

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CURRICULUM VITAE

Name	PERRIG
First name	Marco
Birth	27th of July 1979
Citizenship	Visp (VS) and Brig-Glis (VS)

Education

1994-1999	Matura Typus C, Kollegium Spiritus Sanctus Brig
1999-2002	Study of biology, University of Lausanne
2004-2005	Bachelor of Science, Major in Marine Biology, James Cook University, Townsville (Australia)
2006-2008	Master of Science by research, National Institute of Education – Nanyang Technological University (Singapore) Master thesis entitled: “The use of photo-ID as a tool for estimating population sizes of two siganid species in Singapore”
Since 2010	PhD study at the Swiss Ornithological Institute and the University of Zürich, PhD program: Evolutionary Biology

PUBLICATIONS AND PRESENTATIONS

Publications

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Presentations

2014	“Abwanderungsverhalten junger Steinkäuze (*Athene noctua*) – kurz aber effektiv” Oral presentation at the 147th Deutsche Ornithologen-Gesellschaft e.V., Bielefeld, Germany
2013	“Überlebensraten juveniler Steinkäuze (*Athene noctua*) im ersten Lebensjahr” Oral presentation at the 146th Deutsche Ornithologen-Gesellschaft e.V., Regensburg, Germany
2013	“Natal dispersal in little owls *Athene noctua* – short but effective” Oral presentation at the 9th Conference of the European Ornithologists‘ Union, Norwich, UK
2012	“Der Effekt des Nahrungsangebotes auf die Entwicklung von Nestlingen des Steinkauzes (*Athene noctua*)“ Oral presentation at the 145th Deutsche Ornithologen-Gesellschaft e.V., Saarbrücken, Germany
2012	“Little owl juvenile survival in agricultural landscapes: the role of food availability” Oral presentation at the 3rd European Congress of Conservation Biology, Glasgow, UK