



Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment

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ARTICLE INFO

Article history:

Received 3 November 2017

Initial acceptance 3 January 2018

Final acceptance 9 April 2018

MS. number: 17-00880R

Keywords:

Athene noctua

camera trap

diet

farmland bird

food availability

foraging

habitat effects

parental care adjustments

reproductive success

Food availability is a major characteristic of habitat quality, linking habitats with demographic parameters such as reproductive performance. Parent birds adjust their food provisioning to both habitat-specific food characteristics and the demands of their young. However, because habitat quality and the brood's food intake are often correlated, the underlying mechanisms of adjustments in parental provisioning remain entangled. How the relationship between habitat quality and parental provisioning behaviour affects the quantity of food available to nestlings and the resulting nestling growth and survival is therefore still incompletely established. We experimentally increased the food intake of little owl, *Athene noctua*, nestlings in two habitat types differing in food availability and used unsupplemented broods as controls. The food supplementation experiment allowed us to disentangle the effect of habitat type from the effect of the nestlings' food intake on parental provisioning behaviour. Camera traps recording a series of 10 consecutive images for each parental visit allowed us to quantify visiting rates and diet composition by applying a hierarchical multinomial model explicitly accounting for the observation process. Food supplementation caused parents to switch to smaller food items and to increase visiting rates, resulting in similar biomass brought to nestlings in supplemented and unsupplemented broods. Irrespective of the food supplementation, parents in low-quality habitats delivered 63% of the biomass delivered by those in high-quality habitats. Accordingly, we found an increase in nestling survival rates in response to food supplementation in low-quality habitats, but not in high-quality habitats. Our results show that habitat quality affects the biomass of prey delivered to the brood, whereas the nutritional state of the brood affects prey selection or foraging modes of parents. Reproductive output directly reflected habitat quality in terms of food availability, identifying food as the main factor underlying differential reproduction within and between populations.

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Food availability is a major characteristic of habitat quality, linking habitats with demographic parameters such as reproductive performance. Food limitation creates trade-offs in the allocation of energy to self-maintenance and reproduction (Martin, 1987; Newton, 1998). In altricial birds, the impact of habitat-specific food availability on reproduction is modulated by the parental feeding behaviour (Byholm & Kekkonen, 2008; Tremblay, Thomas, Lambrechts, Blondel, & Perret, 2003). How the relationship between habitat quality and parental provisioning behaviour

affects the quantity of food available to nestlings and the resulting nestling growth and survival is still incompletely established, especially in species feeding on a wide variety of prey.

Food supplementation experiments (providing additional food to nestlings) have been carried out either to study how parents adjust their provisioning behaviour to the nestlings' extra food intake (Hamer, Lynnes, & Hill, 1998; Harding, Van Pelt, Piatt, & Kitaysky, 2002; Santangeli, Hakkarainen, Laaksonen, & Korpimäki, 2012) or to investigate how environmental food constraints contribute to the reproductive performance of wild birds (Byholm & Kekkonen, 2008; Granbom & Smith, 2006; Perrig, Grüebler, Keil, & Naef-Daenzer, 2014; Thorup, Sunde, Jacobsen, & Rahbek, 2010; Wiehn & Korpimäki, 1997). Although the outcome of experimental

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food supplementation is expected to differ in relation to the natural environment, only a few studies have investigated the adjustment of parental provisioning under different environmental conditions. These studies have mostly compared years of contrasting food situations (Karell et al., 2009; Wiehn & Korpimäki, 1997).

In species feeding on a wide variety of prey, parents may not only vary the food delivery rate but also switch between prey types delivered to the brood (Wiebe & Slagsvold, 2015; Wilkin, King, & Sheldon, 2009). In general, offspring development will be influenced by three components of provisioning: prey type, prey size (i.e. energy content) and delivery rate (Browning et al., 2012). Where prey items largely differ in energy content, foraging or handling effort, adjustments in parental provisioning may involve changes in prey selection (Grieco, 2002). Unfortunately, accurate quantification of nestling diet remains difficult, because the proportion of identified prey items parents provide to the nestlings is often biased by the prey type-specific detection probability (Francksen, Whittingham, & Baines, 2016; Robinson; Franke, & Derocher, 2015).

In this study, we aimed to quantify the food delivery rate, prey composition, delivered biomass and the consequences for the reproductive output of little owls, *Athene noctua*, in two breeding habitats that differ in natural food availability (Apolloni, Gruebler, Arlettaz, Gottschalk, & Naef-Daenzer, 2018). In the poorer habitat little owl home ranges are larger (Michel, Naef-Daenzer, Keil, & Gruebler, 2017), and parental foraging trips during chick rearing take longer and go further than in food-rich habitats (Staggenborg, Schaefer, Stange, Naef-Daenzer, & Gruebler, 2017). In both habitats, we conducted a food supplementation experiment. Food supplementation to the nest increases growth rates, body condition and survival of nestlings (Perrig et al., 2014). In this study we addressed the differences between habitats in (1) parental provisioning characteristics in response to the additional food in the nest, and (2) the effect of additional food brought to the nest on nestling survival and, thus, reproductive output. Analysing serial camera trap pictures of feeding visits allowed us to quantify prey delivery rates, the composition of the nestling diet and estimates of delivered biomass, correcting for incomplete prey identification. The results provide insights into the complex mechanisms underlying the relationship between habitat quality and reproductive output and, thus, productivity of populations of altricial birds.

METHODS

Study Species and Study Area

The little owl occurs in a variety of habitats, from natural habitats such as dry hilly steppes and semideserts to anthropogenic habitats such as maquis vegetation, scattered agroforest systems (cork, chestnut, pollard willows, fruit trees) and open agricultural habitats, where it breeds in cavities or burrows (stone or wood, Van Nieuwenhuysse, Génot, & Johnson, 2008). In our German study area, the little owl breeds in tree cavities (and today mainly nestboxes) in open agricultural habitats and orchards. As with many owl species, female little owls are heavier than males (in the breeding season: females 181 g, males 164 g) and both sexes lose weight during chick rearing (Van Nieuwenhuysse et al., 2008). The pairs occupy territories, often for several years (Michel et al., 2017). The clutch size (range one to seven eggs) depends on weather and food availability (Van Nieuwenhuysse et al., 2008). Nestlings become ready to fledge around day 30 after hatching. During incubation and the first 5–7 days after hatching (brooding phase), the female and nestlings are fed by the hunting male. After day 5, females increasingly participate in provisioning behaviour. However, the females dissect large prey in the nest until nestlings can handle it themselves. The little owls' diverse

diet includes small rodents, insects, earthworms and birds. All prey items are delivered one at a time. The main vertebrate prey in central Europe is the common vole, *Microtus arvalis*. Our study was carried out in the district of Ludwigsburg (Baden-Württemberg, Germany: 48°53'N, 9°11'E), a well-populated region of intensively managed farmland interspersed with relicts of traditional standard tree orchards of various sizes. The study population has been part of a ringing scheme for 25 years and currently consists of roughly 220 breeding pairs in an area of ca. 700 km² (H. Keil, n.d.), predominantly breeding in nestboxes mounted on fruit trees.

Habitat Quality

In 2011 and 2012 we selected 56 broods (2011: 25 broods; 2012: 31 broods) in 40 nestboxes in two distinct habitat types within a gradient of agricultural habitats. First, we selected nestboxes on single fruit trees or small tree groups surrounded by large areas of arable fields such as maize, wheat, beet, vegetables and low proportions of permanent grasslands denoted here as 'farmland habitats' (meadows, orchards and gardens in a radius of 180 m around the nest corresponding to <20% of home ranges of ca. 10 ha; arable fields: 80 ± 14%; 2011: 12 broods; 2012: 18 broods). Second, we selected nestboxes on orchard trees in large areas of permanent grassland and structure-rich gardens denoted here as 'grassland habitats' (meadows, orchards and gardens >40%; arable fields: 48 ± 18%; 2011: 13 broods; 2012: 13 broods). Recently, we showed that in our study area the availability of an important prey of little owls, the common vole, is considerably lower in arable fields than in permanent grasslands (Apolloni et al., 2018). Thus, farmland habitats were assumed to provide poor food resources (low-quality habitat) whereas grassland habitats were assumed to provide favourable food resources (high-quality habitat). Twenty-one nestboxes within farmland habitats and 19 nestboxes within grassland habitats entered the study. Only nestboxes with unquestionable assignment to the habitat type were used (farmland: meadows, orchards and gardens <20%; grassland: meadows, orchards and gardens >40%). For details about habitat gradients of broods in the study area and in other German study populations, see Michel et al. (2017) and Staggenborg et al. (2017).

Clutch Size and Age of Nestlings

As in the whole study population, nestboxes were visited monthly from the beginning of April to mid-July and checked for occupation. If signs of occupation were present, we checked the nestboxes weekly until eggs could be recorded and the clutch was full. From the expected hatching date until hatching or brood loss, the nests were visited every 3–5 days. Using developmental illustrations, we visually estimated the age of nestlings through a spy-hole in the nestbox without opening the box (Van Nieuwenhuysse et al., 2008).

Nestling Survival and Experimental Design

From day 10–14 after hatching onwards, all nestboxes were visited every second day up to fledging at ca. 30 days of age. Nestling survival was defined as the survival from eggs to day 28 after fledging. To experimentally increase the nutritional state of nestlings, some broods were supplemented with dead laboratory mice during these visits: a 20 g mouse per nestling during the first six visits and a 30 g mouse during the rest of the visits were deposited in the nestbox. Two synchronous broods in any habitat were denoted as partner broods. One of the two was randomly assigned to the experimental treatment (i.e. food supplementation). For details about the food supplementation experiment and

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