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Linking land cover satellite data with dietary variation and reproductive output in an opportunistic forager: Arable land use can boost an ontogenetic trophic bottleneck in the White Stork *Ciconia ciconia*

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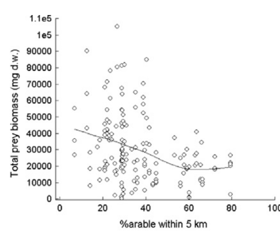
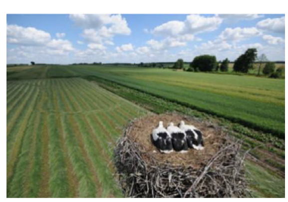
HIGHLIGHTS

- For nestlings the most profitable prey items were Orthoptera and earthworms.
- They probably comprise the staple diet, enabling survival during the first 20 days of life.
- %arable land was negatively correlated with the energy content of the pellets examined.
- Parent birds are unable to satisfy the growing energy demands of nestlings.
- A two-level ontogenetic trophic bottleneck is possible.

GRAPHICAL ABSTRACT





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ABSTRACT

Determining how the progressive loss of resources due to agricultural intensification and habitat degradation affect individual fitness and population persistence is a matter of urgency. Here we explored three major questions in order to extend knowledge of the relationship between reproduction rate, diet and energy intake in White Storks *Ciconia ciconia* based both on our own analysis of pellets and landscape properties sampled in 52 nests in south-western Poland, and published literature data. (1) How many individual prey items are needed to meet the daily energy requirements of nestlings over the brood rearing period? (2) How do the dietary patterns vary under different habitat conditions and what is the spatial scale responsible for these relationships? (3) Is reproductive output related to variations in landscape traits, and is diet variability related to intraspecific competition resulting from colonial breeding? In our estimation, the energy requirements of nestlings during the brood rearing period showed that the most profitable invertebrate prey items were Orthoptera and earthworms. Owing

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Energy requirements
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to the nestlings' gape-size constraint (precluding consumption of vertebrate prey items of the size of Common Voles), these most likely comprise the staple diet enabling survival during the first 20 days of life. The total energy content across all the pellets was a simple function (a negative correlation) of %arable land within a distance of 5 km around the nests. White Storks from nests of high-productivity pairs (with 3–4 fledglings and less %arable around) consumed equal %biomasses of invertebrate and vertebrate prey, while invertebrates prevailed in the diet of the low-productivity pairs. Our results suggest that a two-level ontogenetic trophic bottleneck may explain the low productivity of White Stork pairs in simplified landscapes with predominant arable land use. As a result of this, parent birds are unable to satisfy the growing energy demands of nestlings (1) by gathering a sufficient volume of abundant small-sized prey (early nestlings) and (2) by delivering energetically more profitable vertebrate prey at the time of the diet switch.

1. Introduction

The fundamental aim of ecology is to increase our understanding of how organisms interact with the biotic and abiotic environment (Sutherland et al., 2013). On the other hand, there is a justified conviction that direct processes linked to range contraction and final extinction of certain individual species may never have come to our notice (Purvis et al., 2000; Novacek and Cleland, 2001; Urban, 2015). Hence, we urgently need to discover how the progressive loss of resources due to growing anthropogenic pressure, such as agricultural intensification and habitat degradation, affect the individual fitness and persistence of populations of declining species. In particular, consideration of the role of large-bodied species in a community is of pivotal importance in maintaining natural habitats, especially where a more complete picture of both the diversity and interactions within the community is still lacking (Novacek and Cleland, 2001).

Breeding failures as a result of die-offs of the youngest nestlings in the first few days after hatching is the key factor driving the productivity of a pair of birds (Jovani and Tella, 2004; Granbom and Smith, 2006); consequently, they are ultimately responsible for the productivity of an entire population (Zurell et al., 2015). In principle, mortality of early nestlings depends mostly on the availability of food and its resulting intake (Sasvári and Hegyi, 2001); other factors, too, such as weather, predation, infanticide, parental condition and experience, can affect the survival of the young (Jovani and Tella, 2004; Granbom and Smith, 2006; Slagsvold and Wiebe, 2007). In certain bird species, food composition can vary greatly between different ontogenetic stages, the most pronounced dietary differences being observed between early young and adults/parents (Slagsvold and Wiebe, 2007). Recently, Nakazawa (2015) claimed that almost all organisms on Earth exhibit ontogenetic niche shifts, which causes great phenotypic variation among individuals and is thus regarded as critically mediating community structure and dynamics. In the case of birds, however, this statement is applicable only to certain groups/orders. For instance, it does not refer to raptors (which have the necessary morphological adaptations), which break up large prey items into small pieces of suitable size for their young (Lack, 1946). More importantly, the questions of trophic ontogeny and resulting ontogenetic dietary shifts in predatory species, including birds, have yet to be adequately addressed. This is primarily because species undergoing ontogenetic dietary shifts face the risk of increased competition for resources that delays transitions between feeding stages, which can lead to ontogenetic bottlenecks limiting growth and to starvation in the young (Persson and Brönmark, 2002; Wollrab et al., 2013).

Here we present, to the best of our knowledge, the most comprehensive contemporary dietary and energy study of White Storks *Ciconia ciconia*, a species traditionally classified as a trophic generalist (Schulz, 1998; Dziewiaty et al., 2017). We describe the complex eco-morphological attributes of prey items (including prey groups often overlooked in earlier dietary studies owing to difficulties in quantification, i.e. earthworms and various small invertebrates or insects), and relate them to landscape traits around nests, reproductive success and potential intraspecific interaction resulting from colonial breeding (sensu Nowakowski, 2003; Denac, 2006a; Zurell et al., 2015).

The White Stork is an exceptionally good model species for exploring the above issues for several reasons. First of all, owing to its large body mass, it is the energetically most demanding species of avian predator nowadays inhabiting agricultural areas in central Europe: a pair with only one nestling requires up to 1.6 kg food daily (Profus, 1986; cf. Johst et al., 2001). Secondly, historically since the late 19th century in western and northern Europe, the western White Stork population wintering in West Africa has declined dramatically, mostly due to lower productivity, which is the effect on the one hand of local habitat loss, agricultural intensification and wetland drainage (Bairlein and Zink, 1979; Schulz, 1998; Barbraud et al., 1999; Olsson, 2007), and on the other of a diminished survival rate during winter related to the significant negative trend in the amount of rainfall in West Africa (Kanyamibwa et al., 1993). However, recent changes in the migratory strategy of the western population of the White Stork – switching to residency or short-distance migratory movements within the breeding range in south-western Europe and relying on anthropogenic food (mainly from landfill sites) in winter, as well as intensive reintroduction programmes – has led to an apparent increase in this population (reviewed in Shephard et al., 2015; Gilbert et al., 2016). By contrast, the White Stork's eastern population (wintering in East Africa), part of which inhabits Poland, where it breeds in areas of intensive agriculture in relatively low densities and is characterized by relatively low productivity, has progressively fallen in the last two decades. This appears to be an effect of ongoing agricultural intensification (OTOP, 2016).

The White Stork is a species with a well-defined prey/food spectrum (Schulz, 1998; Dziewiaty et al., 2017) and overall nestling energy budget (Profus, 1986; Johst et al., 2001). Moreover, White Storks always feed their nestlings intact (unfragmented) prey items (Dziewiaty et al., 2017; Romero and Redondo, 2017). During the first days after hatching, young White Storks are fed mainly small (and, when available, slippery) prey items like earthworms, tadpoles, insects and their larvae; larger items are fed from the third week onwards. At age *c.* 5 weeks, mammals and other vertebrate prey are delivered (Tortosa and Redondo, 1992; Lakenberg, 1995; Schulz, 1998). Presumably, young White Storks are to some extent capable of selecting prey of the appropriate size in that they reject items that are too large (sensu Kloskowski, 2001; Moser, 1986). Romero and Redondo (2017) recently observed (in 13 out of 40 feeding events) that parent White Storks often re-ingested prey items that their nestlings had failed to swallow after several unsuccessful attempts. However, earlier data from Poland found evidence of nestling White Storks choking to death after attempting to ingest excessively large prey items, mostly large mammals and snakes (Kosicki et al., 2006). Finally, it is well to recall that White Storks are non-facultative ontogenetic diet