



Diet composition and foraging success in generalist predators: Are specialist individuals better foragers?

Julien Terraube^{a,*}, David Guixé^b, Beatriz Arroyo^{c,d}

^aSection of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland

^bCentre Tecnològic Forestal de Catalunya, Pujada del Seminari s/n, Solsona 25280, Spain

^cInstituto de Investigación en Recursos Cinegéticos (IREC), CSIC-UCLM-JCCM, Ronda de Toledo s/n, 13071 Ciudad Real, Spain

^dCentre d'Études Biologiques de Chizé (CEBC-CNRS), 79360 Villiers en Bois, France

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Abstract

Factors affecting individual diet specialization in generalist populations and the relationship between diet and foraging success remain poorly studied, particularly in terrestrial wide-ranging predators. We studied whether individual variations in diet in Montagu's harrier males (determined through a combination of direct foraging observations and pellet analysis) were associated with patterns of foraging habitat selection and foraging success of 12 radiotracked males during the breeding period. We found important differences in diet composition and breadth between individuals. Diet diversity was negatively related to hunting success: the most efficient individuals in terms of hunting success had the most specialized diet. This study also suggests an important role of individual foraging habitat selection in explaining individual diet, as the proportion of different prey types in the diet was associated with habitat composition within the home range, with higher proportion of those habitats that held higher abundances of their more frequent prey. This study thus provides evidence of individual diet specialization having a knock-on effect on foraging efficiency in a wide-ranging raptor and highlights the role of individual behaviour as a driving force of intra-population niche variation.

Zusammenfassung

Faktoren, die die Nahrungsspezialisierung von Individuen innerhalb der Populationen von Generalisten beeinflussen, und die Beziehung zwischen Nahrung und Fangerfolg sind kaum erforscht, insbesondere bei terrestrischen, weit umherstreifenden Räubern. Wir untersuchten, ob individuelle Besonderheiten in der Nahrung von Wiesenweihen (ermittelt durch eine Kombination von direkten Jagd-Beobachtungen und Gewölle-Analysen) mit Mustern der Wahl des Nahrungshabitats und des Jagderfolgs von zwölf besenderten Männchen während der Brutsaison verknüpft waren. Wir fanden wichtige interindividuelle Unterschiede hinsichtlich der Zusammensetzung und der Breite des Beutespektrums. Die Nahrungsvielfalt war negativ mit dem Jagderfolg verbunden: die erfolgreichsten Jäger hatten das engste Beutespektrum. Diese Untersuchung legt außerdem nahe, dass die individuelle Wahl des Jagdhabitats eine wichtige Rolle bei der Erklärung des individuellen Nahrungsspektrums spielt, da der Anteil der unterschiedlichen Beutetypen in der Nahrung mit dem Habitatsangebot im Aktionsraum einherging, wobei dieser

*Corresponding author. Tel.: +358 468423149.

E-mail addresses: jterraube@gmail.com, julien.terraube-monich@utu.fi (J. Terraube).

durch einen höheren Anteil des Habitattyps gekennzeichnet war, in dem höhere Siedlungsdichten der jeweils häufigeren Beute auftraten. Diese Untersuchung bietet damit einen Beleg dafür, dass individuelle Nahrungsspezialisierung eine Folgewirkung auf die Jagdeffizienz bei einem weit streifenden Räuber hat und unterstreicht die Bedeutung des individuellen Verhaltens als eine treibende Kraft für die Nischenvariation innerhalb von Populationen.

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Introduction

Several studies have highlighted that populations of dietary generalists may be composed of individual specialists (Bolnick et al. 2003; Tinker, Bentall, & Estes 2008; Vander Zanden, Bjornal, Reich, & Bolten 2010; Thiemann, Iverson, Stirling, & Obbard 2011). Araújo, Bolnick, and Layman (2011) suggested that further understanding of individual niche variation is particularly relevant as among-individual differences in competition, predation or parasitism risk may affect population and community dynamics.

A number of factors could be related to the emergence of individual dietary specialization, including morphological differences leading to varying prey capture efficiency (Rincon, Bastir, & Grossman 2007) or individual patterns of space use and habitat-linked variation in prey abundance (McDonald, Olsen, & Baker-Gabb 2003; Quevedo, Svanbäck, & Eklöv 2009). Dietary differences among individuals may be also related to differences in foraging. For example, Woo, Elliott, Davidson, Gaston, and Davoren (2008) showed that individual diet specialization in a Brünich's guillemot (*Uria lomvia*) population was related to foraging behaviour as guillemots specialize on a single foraging strategy across years, regarding flight time, dive depth and dive shape. Additionally, high individual dietary specialization has been related to high foraging success resulting from the use of a few specific foraging strategies on a given prey type, possibly in a consistent way over time (Estes, Riedman, Staedler, Tinker, & Lyon 2003), but this may also lead to poorer foraging success when the preferred prey is not available (Terraube, Arroyo, Madders, & Mougeot 2011).

Overall, the causes and correlates of individual dietary specialization are still insufficiently understood, and the higher ecological performance of individual specialists over generalists remains controversial (Dornhaus 2008; Woo et al. 2008). Furthermore, relatively few studies have empirically examined the relationship between individual diet specialization and foraging success in wide-ranging vertebrate predators, as a consequence of the logistical difficulties of assessing foraging success in this type of species (but see Masman, Daan, & Beldhuis 1988; Tinker et al. 2008; Catry, Alves, Gill, Gunnarsson, & Granadeiro 2014).

The Montagu's harrier (*Circus pygargus*) is a ground-nesting, semi-colonial raptor species characteristic of grassland habitats, which has also adapted well to agricultural habitats in Western Europe (Arroyo, García, & Bretagnolle

2002; Garcia et al. 2011). At a global scale, it is considered a generalist predator (Terraube & Arroyo, 2011), although there may be local specialization in certain prey types, e.g. Montagu's harriers in western France are vole specialists (Salamolard, Butet, Leroux, & Bretagnolle 2000). In most areas, however, diet at the population level is formed by a variety of prey types (Terraube & Arroyo, 2011), but patterns of individual diet variation in those generalist populations, or whether individual specialization is linked with higher foraging success, remain poorly studied.

Our aims in this study were therefore to assess (1) whether diet specialisation levels in a generalist population varied between individuals; (2) whether diet varied according to individual foraging habitat selection; (3) whether diet specialisation was related to foraging success, and in the latter case, whether the effects arise from specialisation *per se* or through specialisation on a particular prey group.

Material and methods

Study area and species

The study took place in the province of Lleida, Catalunya, north-east Spain, from 2002 to 2004. Work was carried out in two Special Protection Areas (SPAs), Anglesola (2002–2004) and Bellmunt (2004), about 15 km apart, covering 8.5 and 28 km² each and containing 12 and 10 breeding pairs of Montagu's harriers respectively in 2004 (25% of the breeding population in Catalunya, and ca. 40% of the breeding population in Lleida that year).

The Montagu's harrier is a species typical of open landscapes. In the study area (as in the majority of Peninsular Spain; Arroyo & García, 2007), the Montagu's harrier nests in crops, mainly in winter cereal during the study years. This species hunts by flying in a low and buoyant manner at constantly low speeds, and the prey is caught in a swoop, rarely on pursuits (Arroyo, García, & Bretagnolle 2004). In the study area, the species feeds on small mammals, birds and insects, captured using the same foraging tactic (Guixé & Arroyo, 2011).

Land-use is mainly agricultural, dominated by winter cereal and alfalfa; additionally, dry orchards (olive and almond trees), irrigated orchards (pear, apple and peach trees), spring-sown crops (mainly corn), woods, fallow land and pastures are also present (Guixé & Arroyo, 2011). For

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