



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

Received 13 January 2014; accepted 21 August 2014
Available online 27 August 2014

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.

© 2014 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Individual specialization; Prey selection; Foraging efficiency; Habitat selection; Montagu's harrier

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

analyses, we grouped habitat in “cereal”, “alfalfa” and “other habitats” (dominated by orchards). Habitat was related to variations in the abundance of the different prey groups, with Mediterranean pine voles *Microtus duodecimcostatus* being more abundant in alfalfa fields and birds being abundant in orchards (D. Guixé, unpubl. data). Additionally, most captures of small mammals were carried out in alfalfa, most captures of insects in cereal and most captures of birds in “other habitats” (Guixé & Arroyo, 2011). In the study area, Mediterranean pine voles exhibit interannual variations in abundance, but these are not marked (based on data from 2004 to 2006, Guixé, Sort & Torre, unpublished data), or at least less marked than in cyclic vole species like *Microtus arvalis*. Bird and insect abundance are also likely to show interannual variations, but these were not measured.

Data collection

The study was based on data from 12 radiotracked males. Eleven of these were attached with tail-mount radios (Ag 357 from Biotrack), and 1 with a backpack (TW-3 from Biotrack). The latter was followed during two consecutive seasons, and an additional male was trapped during two consecutive seasons, giving data on 14 bird-seasons. Overall, four males were monitored in Anglesola in 2002, five in Anglesola in 2003, and in 2004, one male was monitored in Anglesola, and four in Bellmunt.

Taking advantage of the foraging behaviour of harrier species, and of the topographical and landscape characteristics of the study area, we were able to determine the foraging success of individual Montagu's harriers. We followed marked birds continuously from the nest (or from when first observed following the radio signal) up to a hunting point (i.e., an area where a hunting attempt, hereafter strike, was made) with a car, using the extensive track network in the study area, and the radio to relocate the male if visually lost. We kept a safe distance (50 m) between the car and foraging harriers in order not to modify their behaviour. During observations, for each strike observed, we noted the location (and thus distance from nest), the habitat, whether it was successful or not (i.e., whether it resulted in a prey capture), and if it was successful, the type of prey. There could be biases using this method to identify diversity of prey captured if most of the unidentified prey belonged to one prey type, or if it was easier to identify prey in certain habitats. However, overall diet as identified from observations was similar to that identified from pellets and prey remains (Guixé 2003), and there were no habitat differences in the proportion of unidentified prey, so we believe biases are likely to be small.

We aimed to obtain two hunting points per day and more than 40 in total for each monitored bird. Ultimately, number of points per monitored bird ranged between 20 and 58, but only one bird had less than 30. Throughout the three-year study, we obtained a total of 589 points. From these data, we calculated a success rate for each individual (as the number of

captures divided by the number of strikes). For this calculation, we excluded the points where birds had been observed with a prey, but had not been observed hunting previously (e.g., when the radio signal led observers to a perched bird with a prey, or when visibility of strikes prior to capture was limited). Thus, we restricted the data set to 520 points in total (with 253 captures).

Each location (hunting point) was introduced into a GIS (ArcView 3.2), with which we calculated home range using Minimum Convex Polygon (Kenward 2001). Using ArcView also, we crossed the Catalunya Habitat Map (Generalitat de Catalunya, Departament de Medi Ambient i Habitatge, http://mediambient.gencat.net/cat/el_medi/habitats/habitats_cartografia.htm#cd) and home range polygons to determine habitat available within each home range. To estimate habitat selection intensity we used Ivlev's index (Ivlev 1961), comparing the proportion of habitats used with those available (one measure of availability for each SPA area). Ivlev's index is calculated with the expression $IS = (H_1 - A_1)/(H_1 + A_1)$, where H_1 is the proportion of habitat 1 within the home range, and A_1 is the proportion of habitat 1 available in the study area. IS varies between -1 and $+1$. Positive values indicate preference, whereas negative values indicate avoidance.

Prey consumed was evaluated through observations in the field (i.e., through the captures observed in monitored birds). In total, from 382 observed prey, 290 could be identified to prey group: 93 were small mammals, 75 birds and 106 were insects, 16 were other occasional prey (reptiles or bird eggs). To these 290 identified prey we added prey identified from prey remains and pellets found at the nest of the monitored males. These totalled 67 items: 28 were small mammals, 14 birds and 25 were insects, resulting in a total of 357 prey included in subsequent analyses (Table 1). From this data, we calculated a diet diversity index for each individual according to Shannon index: $H' = -\sum(p_i \times \ln p_i)$. The addition of pellet/remain data to those obtained from hunting observations did not bias the results, as (1) cases of necrophagy in Montagu's harriers have never been reported; (2) kleptoparasitism seems to be very rare, particularly among adults (Arroyo & García 2002) and (3) pellets and remains found in nests were collected during incubation and the first two weeks after brood hatching when the male in this species does most of the hunting (Arroyo 1995), and, as specified, the overall proportion of prey in remains and in observations was similar (Guixé 2003).

Statistical analyses

For analyses, for the two males for which we had data from two consecutive years, we excluded data from one of the years (randomly selected). Therefore, analyses were done with $n = 12$.

Individual variations in diet or capture success were analyzed with Chi-square tests (using Minitab 10.2). Factors

Table 1. Diet and foraging parameters of the monitored Montagu's harriers in Lleida. Strikes: hunting attempts; Success: proportion of strikes that resulted in captures; H' : diet diversity (Shannon index).

Individual	Area	Year	Strikes	Success	Total prey	Small mammals	Birds	Insects	H'
Ambient	Anglesola	2003	37	0.49	16	0.25	0.13	0.63	0.391
Ambient	Anglesola	2004	21	0.24	55	0.71	0.13	0.16	0.345
Atten	Anglesola	2002	51	0.68	22	0.41	0.05	0.36	0.379
Bas	Bellmunt	2004	35	0.03	24	0.54	0.08	0.33	0.393
Bell	Bellmunt	2004	31	0.03	19	0.47	0.26	0.26	0.459
Darwin	Anglesola	2002	31	0.77	12	0.17	0.75	0.00	0.223
Donpu	Anglesola	2003	53	0.68	36	0.03	0.33	0.61	0.333
Durrell	Anglesola	2002	54	0.68	18	0.39	0.00	0.39	0.319
Durrell	Anglesola	2003	29	0.66	17	0.65	0.35	0.00	0.282
Felix	Anglesola	2002	45	0.49	31	0.19	0.13	0.48	0.405
Llampec	Bellmunt	2004	20	0.00	21	0.33	0.43	0.24	0.465
Murphy	Anglesola	2003	33	0.54	26	0.42	0.31	0.27	0.469
Pius XII	Anglesola	2003	65	0.57	36	0.03	0.25	0.72	0.296
Somni	Bellmunt	2004	15	0.00	25	0.04	0.60	0.36	0.348

affecting individual variation in diet were analyzed using Generalized Linear Models (GLM), performed in R 2.13.0 (R Development Core Team 2011). We fitted response variables (proportion of small mammals, birds or insects) to a binomial distribution, using two-vector variables (e.g., number of small mammals out of total identified prey for an individual). As we wanted to test whether diet varied according to habitat selected, we compared models including the proportion of certain habitats in the home range, and “year” (to account for potential between-year variation in prey abundance) as explanatory variables. Given that habitat variables are correlated (as they are expressed as %), that sample size is small and that each prey was mainly associated to a certain habitat (see above), and to simplify our initial models, we only included as habitat variables “proportion of alfalfa” for the small mammal models, proportion of “other habitats” for the bird models and “proportion of cereal” for insect models. We compared models including both explanatory variables, with each explanatory variable alone, as well as the null model, in relation to AICc (Burnham & Anderson 2002). Models were ranked in relation to each other using Δ AICc values.

Factors affecting variation in capture success were also analyzed using GLM, with a two-vector variable (number of captures out of number of strikes) fitted to a binomial variable. We compared models including diet diversity, the proportion of each prey type in the diet, or year as explanatory variables, as above. Models compared had a maximum of three explanatory variables (diet diversity, year and the proportion of one prey type).

Results

The most important prey (numerically) were insects (36.7%; $n = 357$), small mammals (33.9%; $n = 357$) and birds (24.9%; $n = 357$). The proportion of these different prey types in the diet varied significantly among individuals ($\chi^2_{22} = 131.4$; $p < 0.0001$), and diet diversity ranged from

0.22 to 0.47. Some harriers consumed primarily small mammals, others primarily birds, and in others the proportion of insects was larger (Table 1), suggesting that some individuals specialized on certain prey types. The two males that were monitored two consecutive years did not have the same diet in different years, although they kept similar diet diversity (Table 1).

Habitat within each home-range was significantly different from what was available in the study area as a whole, but selection differed among individuals (Fig. 1). The males that were monitored two consecutive years selected home ranges with similar habitats in both years (Fig. 1). Overall, the proportion of each habitat type in each home range was positively associated with Ivlev's selection index (Fig. 2).

The proportion of different prey categories in the diet was related to habitat within the home range. In particular, the proportion of small mammals in the diet was higher for males that selected alfalfa in their home ranges, and the proportion of birds was higher for males that selected “other habitats”. The proportion of insects in the diet (the prey type with lowest biomass) was not related to habitat, but varied among years (Tables 2 and 3).

Capture success varied significantly among individuals ($\chi^2_{11} = 26.5$; $p = 0.008$). The best model explaining individual variations in capture success included diet diversity, proportion of small mammals in the diet and year (Table 2): individuals that captured a lower number of prey types were more successful (Fig. 3), as well as those that captured a higher proportion of small mammals (once taking diet diversity and “year” into account) (parameter estimate: 2.58 ± 0.94).

Discussion

Our results show that among Montagu's harriers breeding in the study area, patterns of prey selection as well as diet breadth differed among individuals, confirming that this

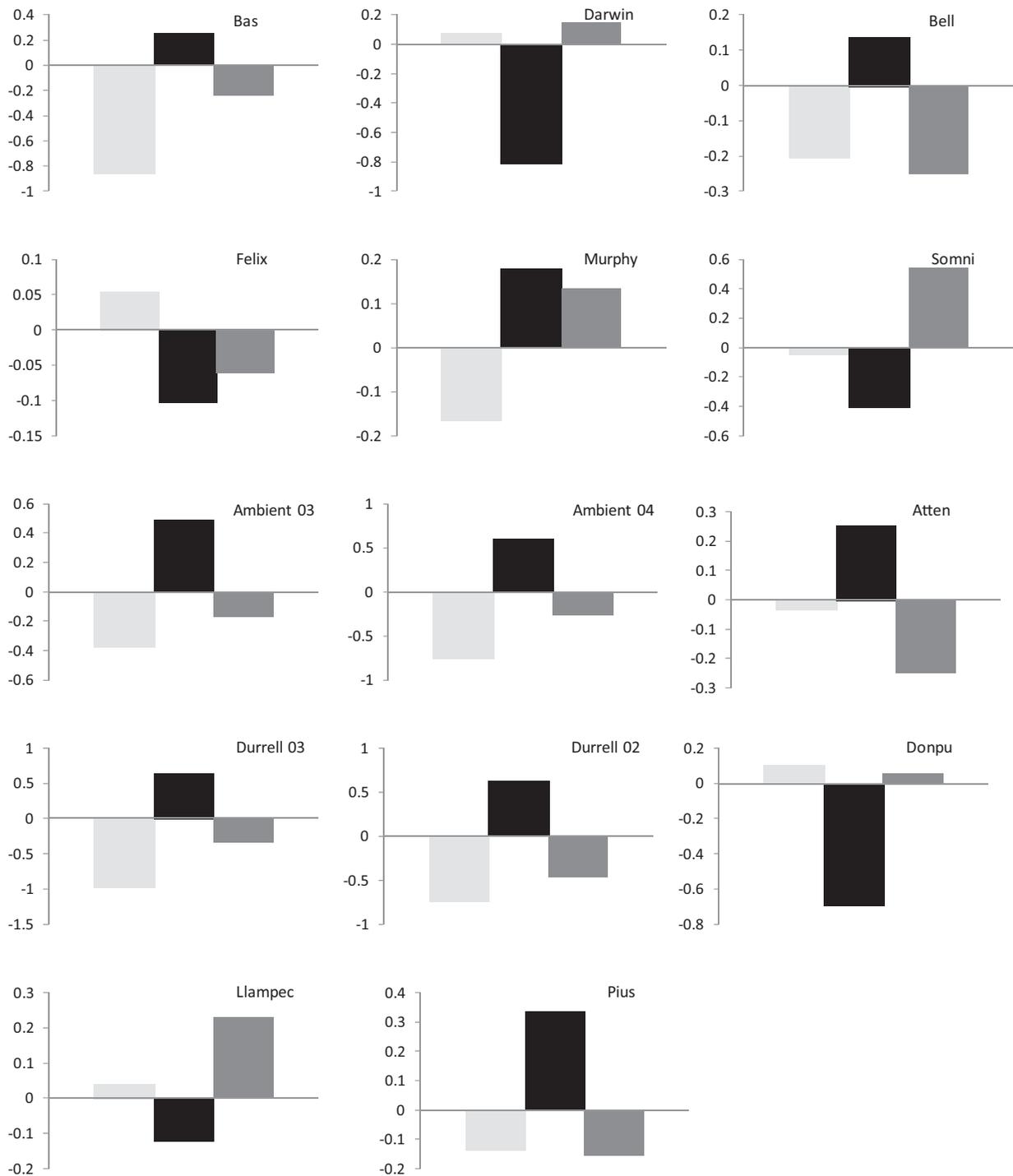


Fig. 1. Ivlev's selection index for each of the tracked individuals. In black, selection index for alfalfa. In light grey, selection index for cereal. In dark grey, selection index for other habitats.

generalist population is composed by individuals with different strategies, including dietary specialists.

Patterns of individual dietary specialization could arise from intra-population phenotypic differences (physiological or morphological), spatial-temporal heterogeneity in the abundance or diversity of foods, cultural influence and early experience or the consequence of density-mediated trade-offs

in resource partitioning (Partridge & Green 1985; Whitfield, 1990; Tinker et al. 2012). At least two of these factors could be behind the individual variability in diet in the Montagu's harriers.

Patterns of individual diet specialization were related to foraging habitat selection, as the proportion of the two main prey groups varied in relation to the main foraging

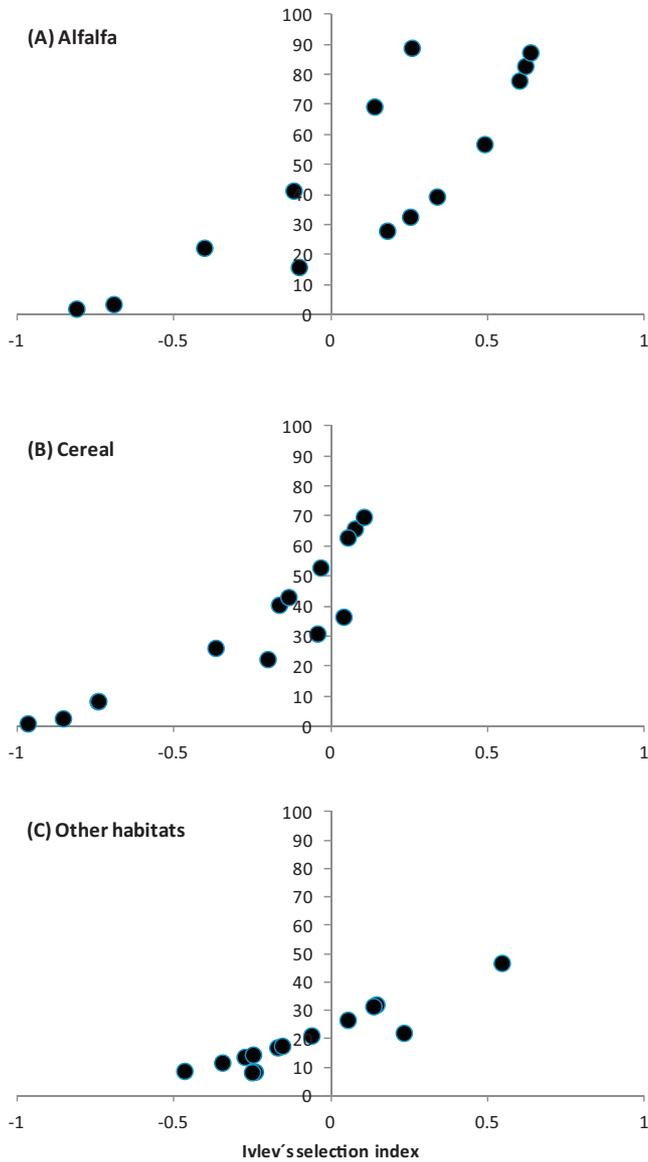


Fig. 2. Relationship between the proportion of different habitats in each home range and Ivlev's selection index for that habitat (comparing with available in the study area), for “alfalfa” (A), “cereal” (B) and “other habitats” (C).

habitats selected by radiotracked males. One explanation for this could be that males take opportunistically the most common prey in their home ranges, which they select for reasons independent of prey availability (e.g., dominance interactions

Table 2. Model-selection results including the number of parameters (*k*) and $\Delta AICc$ comparing relative support for different models (including a null model) describing habitat and year effects on the proportion of different prey types in the diet of Montagu's harriers (Small mammals: proportion of small mammals in diet; Bird: prop. of birds in diet; Ins: prop. of insects in diet; Alfalfa: prop. of alfalfa in home range; Cereal: prop. of cereal in home range; Other habitats: proportion of other habitats in home range; H' = diet diversity).

	<i>k</i>	AICc	$\Delta AICc$
Proportion of small mammals			
Alfalfa	1	85.00	0.00
Alfalfa + Year	3	87.88	2.88
Year	2	110.69	25.69
Null	0	139.86	54.86
Proportion of birds			
Other habitats	1	64.50	0.00
Other habitats + Year	3	69.52	5.02
Null	0	98.74	34.24
Year	2	99.68	35.18
Proportion of insects			
Year	2	77.74	0.00
Cereal + Year	3	88.10	3.35
Cereal	1	86.73	8.99
Null	0	96.58	18.84
Capture success			
H' + SM + Year	4	60.84	0.00
H' + Year	3	63.90	3.06
H' + Ins + Year	4	65.30	4.46
Year	2	66.17	5.33
Year + Ins	3	67.32	6.48
H' + Bird + Year	4	68.51	7.67
H'	1	158.00	97.13
Small mammals (SM)	1	178.90	118.10
Bird	1	193.59	132.75
Null	0	198.68	137.84
Ins	1	201.00	140.20

between neighbouring birds, disturbance, etc.). Alternatively, foraging males could be selecting home-ranges with a higher proportion of habitats holding higher densities of their preferred prey. In the study area, there was clear variation in the abundance of the main prey groups in relation to habitat: passerine birds were more abundant in dry and irrigated orchards (included in our “other habitats” category) than in cereal fields, vole abundance was three times higher in alfalfa than in both cereal and orchards (Guixé 2003), whereas

Table 3. Parameter estimates (\pm SE) for variables explaining variation in the proportion of different prey types. *p*-Values are given in parentheses.

Variables	% Small mammals	% Birds	% Insects
Alfalfa	0.033 \pm 0.005 (0.001)		
Other habitat		0.073 \pm 0.013 (0.001)	
Year (2003)			0.81 \pm 0.31 (0.001)
Year (2004)			-0.53 \pm 0.30 (0.08)

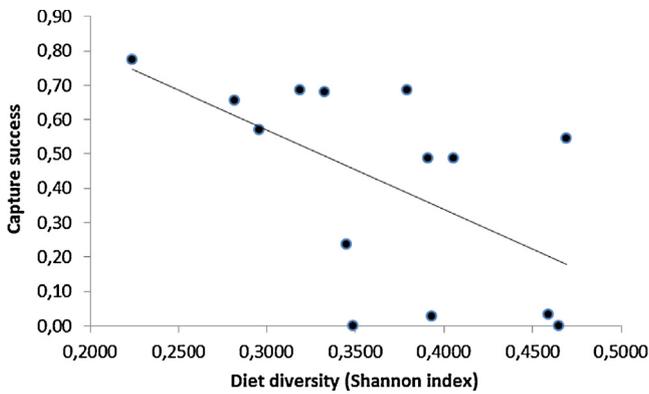


Fig. 3. Relationship between capture success (proportion of strikes that result in a prey capture) and diet diversity for different Montagu's harrier males.

orthopterans (the main insect prey) reach higher abundance in cereal (D. Guixé unpublished data). Therefore, foraging habitat selection may be a good indicator of individual prey choice. Although these results have to be taken with caution due to the small sample size, data obtained for the two males monitored during two consecutive years were consistent with the hypothesis that observed patterns in diet specialization could be related to individual variation in habitat use patterns: they suggest constant patterns of preferred foraging habitats, even if these individuals showed variation in the relative use of particular prey groups, maybe in relation to between-year variations in abundance of different prey types. McDonald and Baker-Gabb (2006) also reported temporal consistency of intraspecific diet specialization at the territory level in Brown falcons (*Falco berigora*).

Morphological traits could also influence particular habitat selection, foraging strategies and ultimately individual foraging success in our study population, as it has been shown in other species (MacNulty, Smith, Mech, & Eberly 2009; Weise, Harvey, & Costa 2010). For example, body size could influence both energetic needs and agility and manoeuvrability, with implications for foraging success on different prey groups, and the individual cost/benefit energetic balance of hunting on prey with different average biomass. Further studies are needed to explore these issues in Montagu's harriers.

Specialist species or individuals appear to be more sensitive to key stimuli (linked to the detection of their preferred prey), whereas generalists respond equally to large quantities of sensory neural inputs (Dukas & Real, 1991). This phenomenon of limited attention helps to understand why specialists are expected to forage more efficiently than generalists, through a search image formation on a given food type, linked to the reduction in encounter and handling time of their preferred prey (Real 1992; Dukas & Kamil, 2001). Strikingly, our results supported this hypothesis, as individuals foraging on fewer prey groups had higher foraging success. Additionally, the proportion of small mammals in the diet was also positively correlated to capture success, which suggests that specialization in small mammals may be more successful

(in terms of foraging efficiency) than specialization in other prey types.

Dietary specialization has been predicted to be most common in food-limited apex predators where inter-specific competition is weak and intra-specific competition is strong (Svanbäck & Bolnick, 2005). Lowland agrosystems in Catalunya host few medium-sized species of breeding raptors (Estrada, Pedrocchi, Brotons, & Herrando 2004), suggesting no significant inter-specific competition for prey in the study area. However, as a colonial species, Montagu's harriers do not defend foraging territories during the breeding period (Garcia & Arroyo, 2002) and males breeding in the same colony may have overlapping home ranges (Guixé & Arroyo, 2011), but breeding in colonies increases intra-specific competition for food (Arroyo 1995). This suggests that intra-specific competition may promote resource partitioning and increase the fitness benefits for males specializing on different prey groups.

It would remain to be tested whether specialization is indeed related to higher fitness in this species. For example, Lescroël et al. (2010) showed recently that in Adélie penguin populations, better breeders were also more efficient foragers than poorer breeders, especially when conditions were challenging. Given that we found a relationship between diet diversity and foraging success, it may be expected that more specialized individuals are also better breeders, particularly those individuals specialized on the most profitable prey in terms of biomass uptake (i.e. small mammals) (McDonald, Olsen, & Cockburn 2004).

One might argue: why some individuals exhibit a generalist foraging strategy in our study population, if individual specialists have higher foraging success? Woo et al. (2008), pointed out that over long periods, with fluctuating prey levels, different foraging strategies may balance out. Recent studies (van de Pol et al. 2009; van de Pol, Brouwer, Ens, Oosterbeek, & Tinbergen 2010) showed also the necessity to consider appropriate time-scales to understand the mechanism by which environmental change affects the evolution and maintenance of diet specialization. Additionally, foraging abilities may be associated to other personality traits in behavioural syndromes (Biro & Stamps, 2008) and different personalities may have different fitness in different environmental conditions (Dingemanse, Both, Drent, & Tinbergen 2004). Studies combining longer-term and other behavioural aspects would be needed to give a reliable impression of temporal variability in fitness components and highlight the possible payoffs of specializing on different prey types.

Acknowledgements

The authors would like to thank the three anonymous reviewers for their valuable comments on earlier drafts of the manuscript. Thanks to all the people that have assisted with this project, especially Ferran Broto, Fermí Sort, Jaume Bonfil, Francesc Pont, Pau Ferrer, Manel Pomarol, Lluís Brotons,

Gerard Bota, David Giral, Anna Ponjoan, Montse Raurell, Juan Bécades, Jordi Bas, Santi Mañosa, Joan Martínez and the rural agents of the Noguera and Urgell districts. We also thank Sean Walls and Ignasi Torre for their recommendations, the Department de Medi Ambient i Habitatge, Regsega and the Centre Tecnològic Forestal de Catalunya for financial and logistic support. BA was supported by a Mobility Grant funded by the Spanish Ministry of Education and Culture (Salvador de Madariaga call, grant number PRX12/00181) while working on this paper in CEBC.

References

- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation: The causes of individual specialisation. *Ecology Letters*, *14*, 948–958.
- Arroyo, B. (1995). *Breeding ecology and nest dispersion of Montagu's harrier Circus pygargus in Central Spain*. University of Oxford (Ph.D. Thesis)
- Arroyo, B., & García, J. T. (2002). Alloparental care and kleptoparasitism in the semi-colonial Montagu's harrier *Circus pygargus*. *Ibis*, *144*, 676–679.
- Arroyo, B., García, J. T., & Bretagnolle, V. (2002). Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Animal Conservation*, *5*, 283–290.
- Arroyo, B. E., García, J. T., & Bretagnolle, V. (2004). *Circus pygargus* Montagu's harrier. *BWP Update*, *6*, 41–55.
- Arroyo, B., & García, J. (2007). *El aguilucho cenizo y el aguilucho pálido en España. Población en 2006 y método de censo*. Madrid: SEO/BirdLife.
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*, 361–368.
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., et al. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, *161*, 1–28.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretical approach* (2nd ed.). New York, NY: Springer-Verlag.
- Catry, T., Alves, J. A., Gill, J. A., Gunnarsson, T. G., & Granadeiro, J. P. (2014). Individual specialization in a shorebird population with narrow foraging niche. *Acta Oecologica*, *56*, 56–65.
- Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *271*, 847–852.
- Dornhaus, A. (2008). Specialization does not predict individual efficiency in an ant. *PLoS Biology*, *6*, e285.
- Dukas, R., & Real, L. A. (1991). Learning foraging tasks by bees: A comparison between social and solitary species. *Animal Behaviour*, *42*, 269–276.
- Dukas, R., & Kamil, A. C. (2001). Limited attention: The constraint underlying search image. *Behavioural Ecology*, *12*, 192–199.
- Estes, J., Riedman, M., Staedler, M., Tinker, M., & Lyon, B. (2003). Individual variation in prey selection by sea otters: Patterns, causes and implications. *Journal of Animal Ecology*, *72*, 144–155.
- Estrada, J., Pedrocchi, V., Brotons, L., & Herrando, S. (2004). *Atlas dels ocells nidificants de Catalunya 1999–2002*. Barcelona: Institut Català d'Ornitologia (ICO)/Lynx Edicions.
- García, J. T., & Arroyo, B. (2002). Intra- and interspecific agonistic behaviour in sympatric harriers during the breeding season. *Animal Behaviour*, *64*, 77–84.
- García, J. T., Alda, F., Terraube, J., Mougeot, F., Sternalski, A., Bretagnolle, V., et al. (2011). Demographic history, genetic structure and gene flow in a steppe-associated raptor species. *BMC Evolutionary Biology*, *11*, 333.
- Guixé, D. (2003). *Caracterització de les àrees de nidificació de l'esparver cendrós a la plana de Lleida. Resultats del radioseguiment i estudi d'alimentació i selecció de l'hàbitat del nucli reproductor d'anglesola*. Unpublished report. Departament De Medi Ambient i Habitatge, Generalitat de Catalunya.
- Guixé, D., & Arroyo, B. (2011). Appropriateness of special protection areas for wide-ranging species: The importance of scale and protecting foraging, not just nesting habitats. *Animal Conservation*, *14*, 391–399.
- Ivlev, V. S. (1961). *Experimental ecology of the feeding fishes*. New Haven, CT: Yale University Press.
- Kenward, R. E. (2001). *A manual for wildlife radio tagging*. Academic Press: London.
- Lescroëil, A., Ballard, G., Toniolo, V., Barton, K. J., Wilson, P. R., Lyver, P. O., et al. (2010). Working less to gain more: When breeding quality relates to foraging efficiency. *Ecology*, *91*, 2044–2055.
- McDonald, P. G., Olsen, P. D., & Baker-Gabb, D. J. (2003). Territory fidelity, reproductive success and prey choice in the brown falcon *Falco berigora*: A flexible bet-hedger? *Australian Journal of Zoology*, *51*, 399–414.
- McDonald, P. G., Olsen, P. D., & Cockburn, A. (2004). Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora*. *Journal of Animal Ecology*, *73*, 683–692.
- McDonald, P. G., & Baker-Gabb, D. J. (2006). The breeding diet of different brown falcon (*Falco berigora*) pairs occupying the same territory over two decades apart. *Journal of Raptor Research*, *40*, 228–231.
- MacNulty, D. R., Smith, D. W., Mech, D., & Eberly, L. E. (2009). Body size and predatory performance in wolves: Is bigger better? *Journal of Animal Ecology*, *78*, 523–532.
- Masman, D., Daan, S., & Beldhuis, H. J. A. (1988). Ecological energetics of the kestrel: Daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labeled water methods. *Journal of Animal Ecology*, *57*, 411–432.
- Partridge, L., & Green, P. (1985). Intraspecific feeding specializations and population dynamics. In R. M. Sibly, & R. H. Smith (Eds.), *Behavioural ecology: The ecological consequences of adaptive behaviour* (pp. 207–226). Oxford: Blackwell Scientific Publications.
- Quevedo, M., Svanbäck, R., & Eklöv, P. (2009). Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology*, *90*, 2263–2274.
- R Development Core Team. (2011). *R: A language and environment for statistical computing*. Vienna, Austria: R foundation for Statistical Computing.
- Real, L. A. (1992). Introduction to the symposium: Behavioral mechanisms in evolutionary biology. *American Naturalist*, *140*, S1–S4.

- Rincon, P. A., Bastir, M., & Grossman, G. D. (2007). Form and performance: Body shape and prey-capture success in four drift-feeding minnows. *Oecologia*, *152*, 345–355.
- Salamolard, M., Butet, A., Leroux, A., & Bretagnolle, V. (2000). Response of an avian predator to variations in prey density at temperate latitude. *Ecology*, *81*, 2428–2441.
- Svanbäck, R., & Bolnick, D. I. (2005). Intraspecific competition affects the strength of individual specialization: An optimal diet theory method. *Evolutionary Ecology Research*, *7*, 993–1012.
- Terraube, J., Arroyo, B., Madders, M., & Mougeot, F. (2011). Diet specialization and foraging efficiency under fluctuating vole abundance: A comparison between generalist and specialist avian predators. *Oikos*, *120*, 234–244.
- Terraube, J., & Arroyo, B. (2011). Factors influencing diet variation in a generalist predator across its range distribution. *Biodiversity and Conservation*, *20*, 2111–2131.
- Thiemann, G. W., Iverson, S. J., Stirling, I., & Obbard, M. E. (2011). Individual patterns of prey selection and dietary specialization in an Arctic marine carnivore. *Oikos*, *120*, 1469–1478.
- Tinker, M. T., Bentall, G., & Estes, J. A. (2008). Food limitation leads to behavioural diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 560–565.
- Tinker, M. T., Guimarães, P. R., Novak, M., Marquitti, F. M. D., Bodkin, J. L., Staedler, M., et al. (2012). Structure and mechanism of diet specialisation: Testing models of individual variation in resource use with sea otters: Network structure of individual resource use. *Ecology Letters*, *15*, 475–483.
- van de Pol, M., Ens, B. J., Oosterbeek, K., Brouwer, L., Verhulst, S., Tinbergen, J. M., et al. (2009). Oystercatchers' bill shapes as a proxy for diet specialization: More differentiation than meets the eye. *Ardea*, *97*, 335–347.
- van de Pol, M., Brouwer, L., Ens, B. J., Oosterbeek, K., & Tinbergen, J. M. (2010). Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution*, *64*, 836–851.
- Vander Zanden, H. B., Bjornal, K. A., Reich, K. J., & Bolten, A. B. (2010). Individual specialists in a generalist population: Results from a long-term stable isotope series. *Biology Letters*, *6*, 711–714.
- Weise, M. J., Harvey, J. T., & Costa, D. P. (2010). The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, *91*, 1004–1015.
- Whitfield, D. P. (1990). Individual feeding specialisations in wintering Turnstone *Arenaria interpres*. *Journal of Animal Ecology*, *59*, 193–211.
- Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology*, *77*, 1082–1091.

Available online at www.sciencedirect.com

ScienceDirect