

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

Julien Terraube^{1*}, David Guixé², & Beatriz Arroyo^{3,4}

1- Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland.

2- Centre Tecnològic Forestal de Catalunya, Pujada del Seminari s/n, Solsona 25280.

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

4-Centre d'Etudes Biologiques de Chizé (CEBC-CNRS), 79360 Villiers en Bois, France

* Corresponding author:

Julien Terraube

Section of Ecology, Department of Biology, University of Turku, FIN-20014 Turku, Finland;

Email: jterraube@gmail.com;

Phone number: +358468423149.

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 suggested 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 predator and highlights the role of individual behavior as a driving force of intra-population niche variation.

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 by individual specialists (Bolnick et al. 2003; Tinker et al. 2008; Vander Zanden et al. 2010; Thiemann et al. 2011). Araújo et al. (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 et al. 2007), or individual patterns of space use and habitat-linked variation in prey abundance (McDonald et al. 2003; Quevedo et al. 2009). Dietary differences among individuals may be also related to differences in foraging. For example, Woo et al. (2008) showed that individual diet specialization in a Brünnich'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 et al. 2003), but this may also lead to poorer foraging success when the preferred prey is not available (Terraube et al. 2011).

Overall, the causes and correlates of individual dietary specialization are still insufficiently understood, and the higher ecological performance of individual specialists over generalist 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 et al. 1988; Tinker et al. 2008; Catry et al. 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 et al. 2002). At a global scale, it is considered as 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 et al. 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), distant ca. 15 km, 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 mainly by flying in a low and buoyant manner at constantly low speeds, and the prey is caught in a swoop, rarely on pursuits (Arroyo et al. 2004). In the study area, the species feeds on small mammals, birds and insects (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 also 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 2004-2006, 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 also 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 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 on 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 in 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). Additionally, 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: $H = -\sum (p_i \ln p_i)$. The addition of pellet/remain data to those obtained from hunting observations did not bias the results, as they 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), but in contrast allowed us to increase sample size for each individual.

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 analysed with Chi-square tests (using Minitab 10.2). Factors affecting individual variation in diet were analysed using Generalized Linear Models (GLM), performed in R 2.13. 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 among them (as they are expressed as %), that sample size is small, and

that each prey was mainly associated to a certain habitat (see above), to simplify our initial models, as habitat variables we only included proportion of alfalfa for the small mammal models, for the bird models only proportion of “other habitats”, and for insect models only proportion of cereal. We compared models including both explanatory variables, with each explanatory variable alone, as well as the null model, in relation to AICc (Burhnam & 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

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 specialised 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 MCP 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 to 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, 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 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 two main prey groups in the diet varied in relation to the main foraging habitats selected by radiotracked males. One explanation for this could be that males take opportunistically the most common prey in the home ranges, which they select for reasons independent of prey availability (e.g. dominance interactions 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 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.

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 et al. 2009; Weise et al. 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 et al. 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 in this colonial species.

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).

One might argue: why some individuals exhibit a generalist foraging strategy in our study population, if individual specialist 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, 2010) showed also the necessity to consider appropriate time-scale 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 and Stamps, 2008) and different personalities may have different fitness in different environmental conditions (Dingemanse et al. 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.

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Table 1. Diet and foraging parameters of the monitored Montagu's harriers in Lleida. Strikes: hunting attempts; Success: proportion of strikes that resulted on captures; Birds-Sm-Ins: proportion of birds, small mammals or insects among total prey captured; H: diet diversity (Shannon's 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

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

7
 8

	k	AICc	$\Delta AICc$
Small mammal proportion			
Alfalfa	1	85.0	0.00
Alfalfa + year	3	87.88	2.88
Year	2	110.69	25.69
Null	0	139.86	54.86
Birds proportion			
Other hab.	1	64.50	0.00
Other hab. + year	3	69.52	5.02
Null	0	98.74	34.24
Year	2	99.68	35.18
Insect proportion			
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	158.0	97.13
Sm.	1	178.9	118.1
Bird	1	193.59	132.75
Null	0	198.68	137.84
Ins.	1	201.0	140.2

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12 Table 3. Parameter estimates (\pm SE, P value in brackets) for variables explaining variation
13 in the proportion of different prey types.

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Variables	% Sm. 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)

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

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23 Figure 2. Relationship between the proportion of different habitats in each home range and
24 Ivlev's selection index for that habitat (comparing with available in the study area), for
25 alfalfa (above), cereal (centre) and "other habitats" (below).

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

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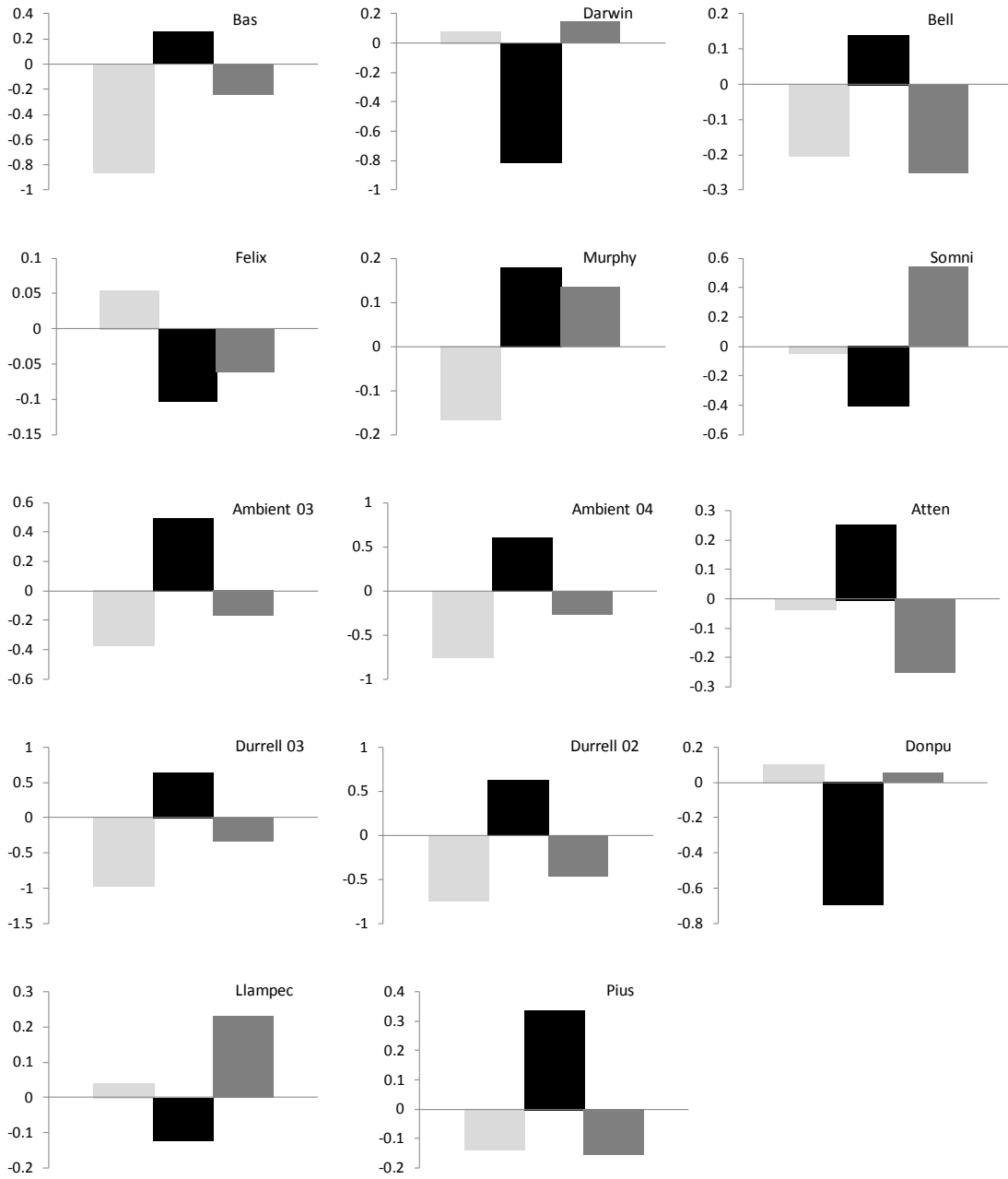
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33 Figure 1.

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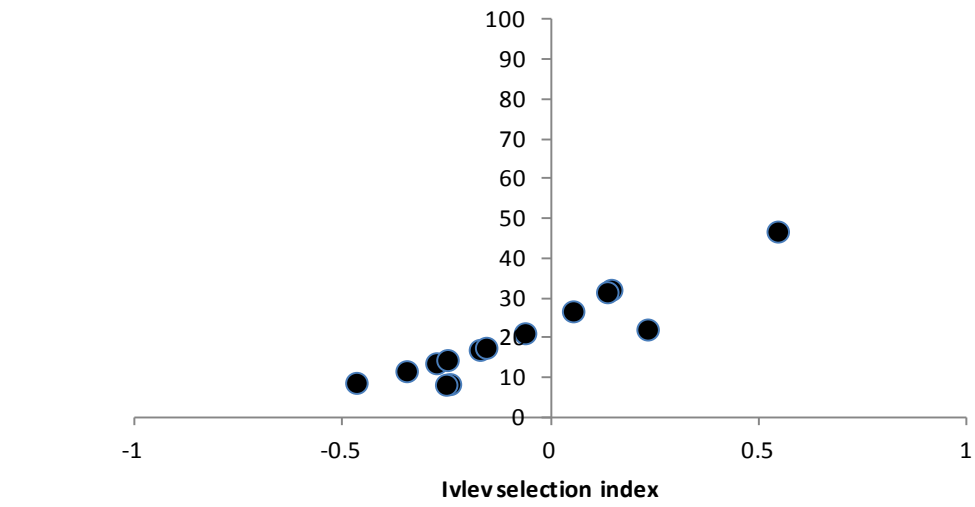
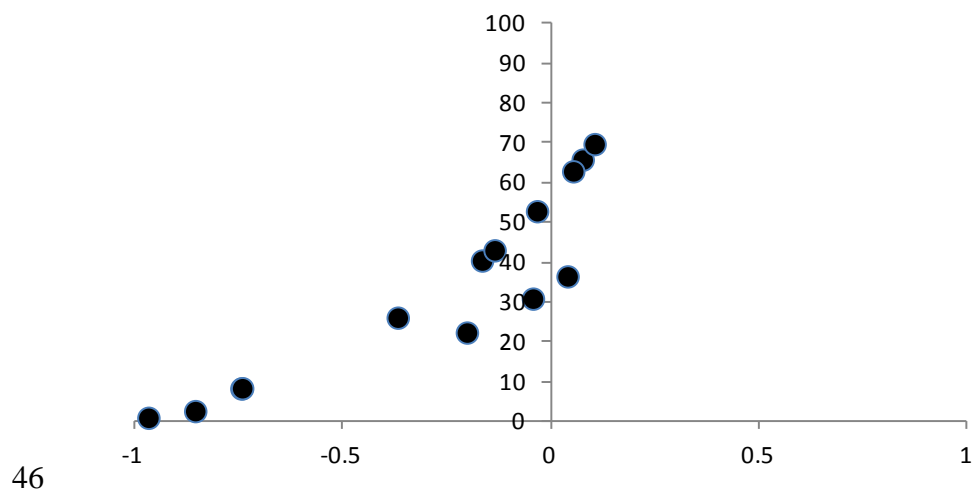
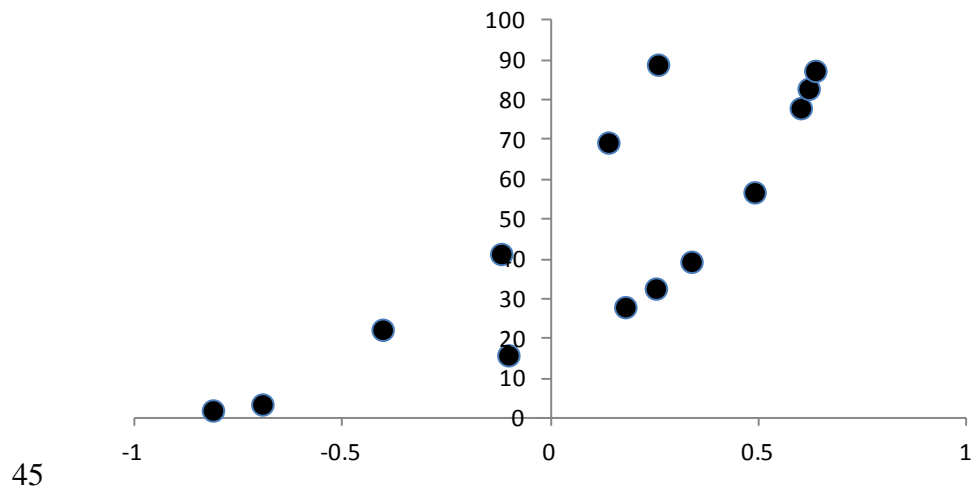
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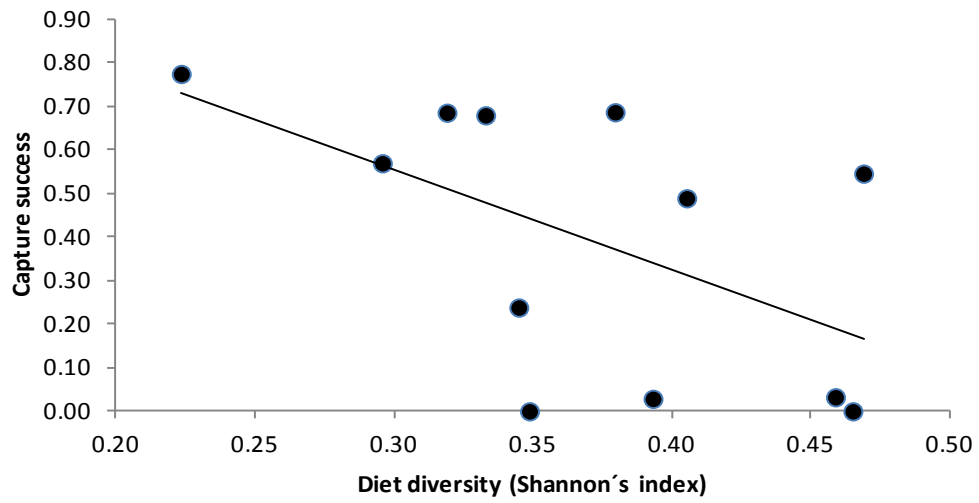
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42 Figure 2.
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Figure 3.



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