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ORIGINAL PAPER

Variation in White Stork (*Ciconia ciconia*) diet along a climatic gradient and across rural-to-urban landscapes in North Africa

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Abstract Assessing diet composition of White Storks (*Ciconia ciconia*) breeding under North African conditions provides key information to understanding its trophic niche for conservation purpose. Since, climate controls productivities of foraging habitats and thus food availability for predators, this study examines how Storks' diet parameters varied following a climate gradient along with rural-to-urban landscapes in north-eastern Algeria. Feeding strategies to cope with severe conditions were discussed in light of climate aridity and urbanization and how these influence reproduction, population dynamics and distribution. While invertebrate prey accounted for 94 % of ingested individuals, the biomass intake was dominated by chicken remains scavenged from rubbish dumps (67 %) and small mammals (14 %). Generalized linear models revealed that prey numbers varied significantly between climatic regions and landscapes types, but no significant differences were observed for other dietary parameters, including prey biomass. The study showed high dietary similarity between study climates and landscapes, mainly among rural and urban colonies located in semi-arid and sub-humid areas, which differed from those in suburban and arid climate. Rarefaction and extrapolation curves indicated that prey species richness in White Stork diets was expected to be higher in urban colonies located in sub-humid climate. Despite low prey species diversity in arid regions, the White Stork demonstrates a broad trophic niche, which could be due to supplementary feeding from human refuse. This study suggests that regardless of the climate or landscape, White Storks ensure a constant food intake, despite prey biomass fluctuations, by adapting their diet. Foraging in diverse habitats, including trash dumps, ensures a sufficiently balanced diet to meet nutritional requirements.

Keywords White Stork *Ciconia ciconia* · Diet composition · Feeding ecology · Trophic niche · Drylands · Rubbish dumps

Introduction

Modifications of climate and landscape due to urbanization affect birds through modifications in the habitat and food supply, which change ecosystem processes, including changes in biotic interactions like intra- and interspecific competitions, predation, and illnesses (Chace and Walsh 2006; Fuller et al. 2012). Urbanization changes local climates through modifications of clouds and precipitation, but also through changes in atmospheric radiation and precipitation as initiated by anthropogenic aerosols. These climate modifications are connected to population density, land use, level of industrialization, building compactness, seasons, and predominating environmental forcing (Jin et al. 2005). Moreover, urban areas provide also additional and permanent foraging and nesting opportunities (Alberti 2005; Mainwaring 2015; Chenchouni 2016; Chenchouni et al. 2016), which positively affect urban-adapted and urban-exploiter species (Chace and Walsh 2006; Fuller et al. 2008).

Because local climatic conditions are critical in controlling food resources, which in turn affect reproductive performance, the effects of climate on the diet and reproduction of the White Stork have been explored (Jovani and Tella 2004;

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Tryjanowski et al. 2009). Studies have investigated the influence of climate factors and variability in food availability at foraging/breeding habitats on reproductive patterns (Tortosa et al. 2003; Tryjanowski et al. 2005a; Denac 2006; Djerdali et al. 2008; Kosicki 2012; Si Bachir et al. 2013). In addition, Si Bachir et al. (2013) reported that levels of urbanization affected the breeding success and population densities of the species.

Several studies of the impacts of climate conditions on White Stork have started to explore how climate patterns affect breeding success and individual survival through changes in habitat primary production (Schaub et al. 2005) and prey availability (Tryjanowski and Kuzniak 2002) following severe climatic/weather events (Tryjanowski et al. 2005a, b, 2009; Tobolka et al. 2015). These studies document how climate/weather modifies breeding parameters and population dynamics including nestling survival through change in climate, food supply and nest sites. Most studies have not asked directly questions on the effects of climate patterns on diet composition and feeding ecology, but instead they investigate how weather conditions affect White Stork productivity and nestling survival and their inferences for population dynamics (Tryjanowski et al. 2009; Kosicki 2012) while insinuating that modifications in feeding/foraging ecology are interlocutors in the process. With this in view, climate change also induces an uphill shift in the distribution and nesting of the White Stork (Tryjanowski et al. 2005b), which causes changes in foraging niches and opportunities between different climatic regions (Chenchouni 2016) and thus influences breeding success (Kosicki 2010; Chenchouni et al. 2016).

Research on food composition plays a vital role in assessing foraging habitats and defining the trophic niches of species for conservation purposes (Alonso et al. 1991). Birds in general, and waterbirds in particular, are good indicators of rapid changes in environmental conditions due to climate change, urbanization or changes in landscape configuration and function (Durant et al. 2007; Gregory and Strien 2010; Bensizerara et al. 2013). The abundance of available food resources appears to be one of the main factors limiting the densities of animal populations (Karasov 1996; Janiszewski et al. 2014), especially in birds (Brasher et al. 2007; Tryjanowski et al. 2009; Crampton et al. 2011).

Studies of the diet of White Storks (*Ciconia ciconia* Linnaeus 1758) have shown that it is an opportunistic predator (Vrezec 2009). Most of these studies are based on the analysis of digested remains found in regurgitated pellets (Mužinić and Rašajski 1992). Even though the analysis of pellets has some caveats, this technique has been successfully used in the past and is a less invasive technique than other options such as direct analysis of gut contents (Chenchouni 2014). However, it is as relevant as some techniques that force regurgitation using chemical components (Zduniak 2005).

The White Stork has been extensively studied in Europe (Tryjanowski et al. 2009). However, in North African breeding grounds, information on its diet is scarce and mostly limited to the northern areas of Algeria (Boukhemza 2001; Sbiki 2009; Djerdali et al. 2016). This makes data from the African range of this species very useful ecologically in terms of establishing a comprehensive conservation plan since data from other North African countries is scarce (Ciach and Kruszyk 2010). Previous studies have mainly focused on (1) dietary composition based on pellet analyses (Boukhemza et al. 1995); (2) food resource availability and composition (Boukhemza et al. 2004, 2006); (3) foraging habitat use (Boukhemza et al. 2006; Chenchouni 2016); and (4) feeding strategies during different breeding stages (Chenchouni et al. 2015). White storks have been reported to feed and rest at rubbish dumps in North Africa (Morocco, Egypt), as well as in the Middle East and the Arabian Peninsula (Ciach and Kruszyk 2010). This behaviour is also common in Algeria (Chenchouni et al. 2015; Djerdali et al. 2016). To my knowledge, there is no study addressing variation in White Stork dietary patterns along a climatic gradient, including arid and semi-arid areas, nor comparing rural to urban landscapes. Furthermore, the influence of urbanization on wildlife, including birds, remains poorly investigated at the North African scale.

In a global warming scenario (Durant et al. 2007), mismatches can occur between local peaks in food abundance and the timing of breeding, with severe consequences for reproductive success (Van Der Jeugd et al. 2009; Thomas et al. 2001). Since, climatic conditions are subject to spatial and temporal variations that affect foraging habitats and food resources, White Storks are likely to modify their feeding efforts to maintain high levels of energy consumption and fitness whatever the climate, thereby ensuring high reproductive success. Under different climatic conditions, the White Stork is expected to adjust its food intake according to dietary characteristics (quantity, quality and availability), e.g. either by consuming a large number of prey under mesic climate, targeting prey of higher biomass in xeric climate areas where prey are scarce, or selecting prey higher in nutritional value in particular foraging habitat with high productivity.

The climate along with landscape type and structure, affects the productivity and breeding numbers of birds, through changes in water availability and agricultural conditions (Tryjanowski et al. 2005a, b; Ramo et al. 2013; Si Bachir et al. 2013). Moreover, birds select heterogeneous productive habitats (Johst et al. 2001; Tsachalidis and Goutner 2002; Boukhemza et al. 2006; Janiszewski et al. 2014) that offer a range of food resources varying in quality, abundance and availability (Kosicki et al. 2006), which affects breeding success (Tryjanowski and Kuźniak 2002; Tortosa et al. 2003; Massemin-Challet et al. 2006). To properly understand whether aridity and urbanization influence White Stork diet, it is essential to describe dietary composition across climates and landscapes. Here, I assess if diversity in White Stork diets decrease in urban environments compared to natural-rural habitats and if dietary composition (in terms of diversity and quantity) varies according to habitat productivity (as influenced by climate). This study examines the variation in biodiversity and similarity of prey communities found in White Stork diet across a mesic-xeric climatic gradient and along rural-to-urban areas.

Material and methods

Study area and colonies

The diet of nesting pairs of White Storks in rural and urban areas of Batna (north-eastern Algeria), where the bulk of the White Stork population lives (Si Bachir et al. 2013), was studied using pellet analysis. Eight White Stork colonies located in different climatic areas (sub-humid, semi-arid and arid) were surveyed (Fig. 1): (1) Merouana, (2) Oued El Ma, (3) Seriana, (4) K'sar Belezma all experience a cold sub-humid climate; (5) Ferme Riche, (6) Bouachaoune, (7) Chemora have a cool semi-arid climate; and (8) N'Gouas presents a cool arid climate. These broad climatic differences in the study area are mainly due to the large range in elevations and the specific location between the Mediterranean Sea (~115 km to the north) and Sahara Desert (~90 km to the south) (Chenchouni et al. 2010).

Climate information for each colony site was generated based on interpolations of long-term weather data from the nearest ten meteorological stations around the study colony in question. Interpolations were carried out using the nearest neighbour method of the climate software package New_LocClim version 1.10 (http://www.fao.org/nr/climpag/pub/en3_051002_en.asp). Although these interpolations are more suited for broad-scale areas, some climatic differences were observed between some of these White Stork study sites, as follow:

Climate characteristics in Merouana, Oued El Ma, K'sar Belezma and Seriana were quite similar. A second group of climatically similar colonies includes the Ferme Riche, Bouachaoune and Chemora sites. Finally, these two sets of colonies have different climate characteristics than those of the colony of N'Gouas. The Budyko's radiation index of dryness (Budyko 1974) (range, 2.88–2.94) indicated a semi-arid climate in the first set of colonies, whereas the rest of colonies are classified as desert with Budyko's radiation index of dryness varied between 3.48 and 3.86. However, the De Martonne's index (De Martonne 1925) revealed that the climate in Merouana, Oued El Ma, K'sar Belezma and Seriana is dry sub-humid, whereas it is semiarid in Ferme Riche, Bouachaoune, Chemora and N'Gouas (Appendix Table 6). In all study colonies, the estimated precipitation deficit showed values greater than 688 mm/year, which is higher than the annual rainfall recorded in the region. The climatic net primary production (NPP) of these sites ranges between 582 and 741 g DM/m^2/year, with precipitation, rather than temperatures, thought to be the main factor limiting NPP in such North African habitats (Bradai et al. 2015).

The colonies of Bouachaoune, K'sar Belezma, and Ferme Riche are located in rural landscapes, the colonies of Oued El Ma and Seriana lie within suburban landscapes, while the colonies of Chemora, Merouana and N'Gouas are situated in urban areas. This classification was based on the extent of urban areas, human population size, and adjacent agricultural and natural landscapes. Urbanized areas consisted of built-up conurbations with a population of 20,000 or more. The population sizes of Merouana, N'Gouas and Chemora was about 41,125, 31,920 and 20,369 inhabitants, respectively, at the time of study (data provided by *DPAT, Direction de Planification et d'Aménagement du Territoire, Batna City*) (Appendix Table 6). Rural areas were considered any place with less than 1,000 inhabitants living in scattered houses situated within a matrix of natural and/or agricultural landscapes. Suburban territories were those that did not fit either of these latter two classifications.

Collection and analysis of pellets

In late January, old pellets were removed from nesting sites constructed on top of different support-types (e.g. roofs, electricity pylons) at each study colony before the arrival of breeding White Storks. Regurgitated pellets were then collected at regular intervals (every 2 weeks) throughout the reproductive period from early February 2011 to late July 2011. Out of more than 200 total pellets collected during that period, only 87 regurgitated pellets from breeding adults were analysed during this study. Only non-fragmented pellets were analysed, which were selected based on their size (large length and breadth) and oval shape. Small pellets from chicks were not analysed for this study. Of these 87 pellets, 36 were from the sub-humid zone, 40 from the semi-arid region and 11 from arid areas. Similarly, divided among landscapes, these 87 pellets were represented by 14 from suburban landscapes 37 from rural and 36 from urban areas. We employed sample-based rarefactions to compare diet richness (Colwell 2013) (see 'Extrapolation of species richness' section).

Pellets were separated and analysed using standard methods (Duffy and Jackson 1986; Rosenberg and Cooper 1990). Prey remains were identified to genus and/or species level (or at least to family level) using a binocular stereomicroscope and identification guides/keys.

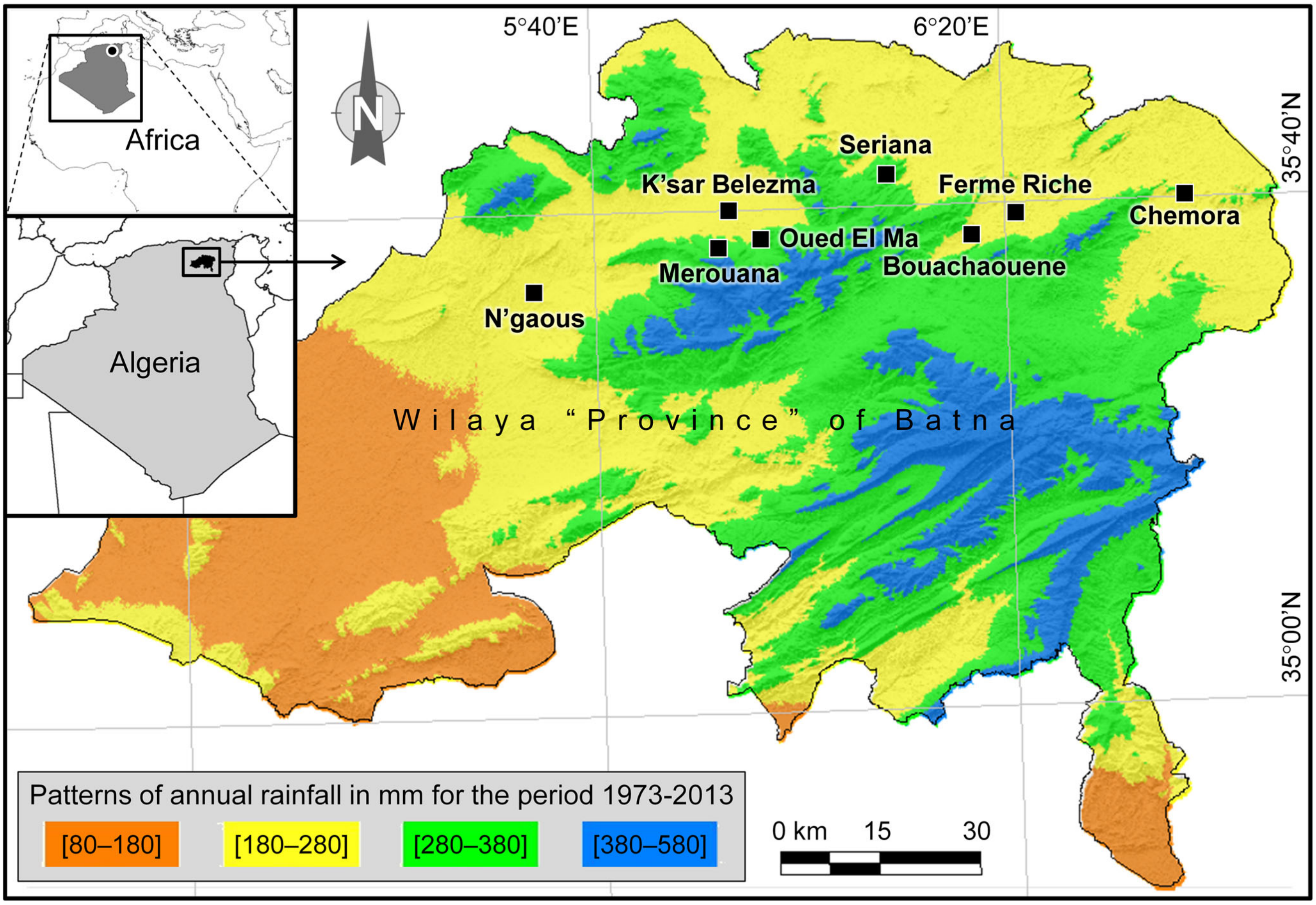


Fig. 1 Interpolated annual rainfall map of Batna (north-eastern Algeria) and geographical locations of the eight sampled colonies of White Stork (*Ciconia ciconia*). Interpolations are based on long-term rainfall data of the meteorological station of Batna

Biodiversity analyses

Observed prey biodiversity

The pellet was used as a unit of measure for the following dietary parameters. The number of individual 'prey-items' (ni) was determined for each prey species found in each pellet, and the prey frequency 'PF' was calculated as the proportion of the prey species i of the total number of individuals (N). Observed species richness 'S' was estimated as the total number of prey species identified (Magurran 2004). Mean N per pellet (Nm) and mean S per pellet (Sm) were the average numbers of individuals and prey species, respectively, observed in pellets. Prey biomass (B) was evaluated as the weight of 'ni' individuals of a prey species divided by the total weight of all prey individuals (Vivien 1973). Prey biomass was obtained from previous studies conducted under the same ecological conditions in the study area (Ghenam and Si Bachir 2011; Chetara and Mechouma 2012; Chenchouni 2014). For both invertebrate and vertebrate prey species, fresh weight was used to determine the biomass of the identified prey species. Prey frequency (PF) and prey biomass (B) were calculated for pellets pooled according to climate zone or landscape type. For these latter two parameters, data are presented at the level of order to facilitate comparisons between studies (Duffy and Jackson 1986). Pearson's Chi-square tests (χ^2) were used to compare values of PF and B of the main prey groups (defined as taxonomic orders of prey) among study climatic areas and landscape types.

The diversity of White Stork diets was measured using Shannon's index ($H' = -\sum(\text{pi} \times \log_2 \text{pi})$) and Shannon's evenness ($E = H'/H_{\max} \times 100$, with $H_{\max} = \log_2 S$), where pi is the proportion of the prey species i in the diet (Magurran 2004). Evenness values vary from 0 (representing a dietary specialist) to 100 % (indicating a dietary generalist). In addition, the Food Niche Breadth (FNB): FNB = $1/\sum \text{pi}^2$ was applied to assess prey diversity and the trophic niche of the species. The values of this index range from 1 to S (i.e. the total number of observed prey species), with larger values indicating a wider feeding niche dimension (Levins 1968). A new ratio (FNB/S) was adapted to express accurately the food niche breath of the species. The ratio FNB/S varies between 0 (representing a narrow trophic niche) and 1 (indicating a broader feeding niche).

Estimates of prey species richness

The program EstimateS 9.1.0 (Colwell 2013) was used to compute estimated prey species richness (S_{est}). S_{est} was assessed using the most precise and the least biased estimators (Brose and Martinez 2004). The following asymptotic species richness estimators were applied: (1) S_{est} (analytical) that provides the expected number of prey species among a given number of samples (Colwell et al. 2012); (2) the first-order Jackknife estimator of species richness ($S_{(Jack\ 1)} = S + Q_1((m–1)/m)$) (Heltshe and Forrester 1983); and (3) Chao 2 estimated species richness ($S_{(Chao\ 2)} = S+((m–1)/m)(Q_1^2/2Q_2)$) (Chao 1987); where S is the total number of prey species observed in all pellets pooled, m is the total number of pellets analysed, and Q_1 and Q_2 are the frequencies of uniques (prey species that occur in only one pellet) and duplicates (species that occur in only two pellets), respectively. The numbers of uniques and duplicates, as well as values of species richness estimators, are given as mean (±standard deviation 'SD') based on 100 runs of randomizations (Colwell et al. 2012). Moreover, four indices of species diversity were simultaneously computed using EstimateS: (1) Fisher's alpha (the alpha parameter of a fitted logarithmic series distribution); (2) Shannon diversity index (H'); (3) the inverse form of Simpson diversity index ($1/I_s$) where $I_s = (\sum ni(ni - 1))/N(N - 1)$; and (4) Hill numbers = $(1/I_s)/\exp.(H')$ (Magurran 2004).

Extrapolation of species richness

In order to deal with the varying sample size between climates and landscapes and to equalize the information content of samples, rarefaction and extrapolation curves were linked based on a set of appropriate statistical sampling models (Colwell et al. 2012; Colwell 2013). Species richness was extrapolated to facilitate comparison of the richness of rarefied reference samples (i.e. the numbers of pellets). Extrapolations were conducted to a sample size of 300 pellets for the entire study area and for each climate and landscape. Interpolations of S_{est} are given with the lower and upper bounds of a 95 % confidence interval.

Model of raw data is multiple-sample-based-data (batch input, including climates and landscapes of colony sites: see Table S2: https://dx.doi.org/10.6084/m9.figshare.2008671) used in species richness estimations and interpolations. More details on rarefaction, extrapolation, species richness estimators, and indices of species diversity are available in Colwell (2013).

Spatial similarities of prey communities

In order to estimate shared species richness between climatic regions and landscape types, several similarity indices were computed. These included qualitative similarity estimates using the classic Jaccard and Sørensen indices, and also quantitative approaches such as raw and estimated Chao's Jaccard indices, raw and estimated Chao's Sørensen indices, the Morisita–Horn index and the Bray–Curtis index (Magurran 2004; Chao et al. 2005). The free software EstimateS was applied in calculation of all shared species richness and similarity statistics (Colwell 2013). The model of raw data used for the analysis of similarities was Format 1 of Single-Sample-Based-Data 'Filetype 1' (see Table S3 at https://dx.doi.org/10.6084/m9.figshare.3463310 for climatic regions and Table S4 at https://dx.doi.org/10.6084/m9.figshare.3463313 for landscape types).

Statistical analyses

Generalized linear models (GLMs) were performed to model the effects of climate and landscape types on each dietary parameter (N, B, S, FNB, FNB/S, H', H_{max}, E) recoded within each pellet. The effect of the interaction 'climate × landscape' was included in every GLM. Parameters represented by count data (N, S) were modelled using a Poisson distribution error and log link function, whereas the remaining dietary parameters (B, FNB, FNB/S, H', H_{max}, E) were tested with a Gaussian distribution and Identity link (Myers et al. 2012). Type-II analysis-of-variance was used for each GLM to emphasize the effects of factors (climate, landscape, climate × landscape) and to downplay the analysis of deviance (likelihood-ratio tests 'LR'). Type-II tests were applied because all of the predictors in the GLMs were factors. The software R was used for statistical modelling (R Core Team 2015).

Results

Diet composition and prey richness

Chi-squared tests revealed that prey frequencies of taxonomic prey orders differed significantly, both between climatic areas ($\chi^2 = 45.41$, $df = 24$, $P = 0.005$) and between landscape types ($\chi^2 = 70.15$, $df = 24$, $P < 0.0001$). However, analysis of contingency tables showed no significant difference in biomass values for these prey groups either among climatic areas ($\chi^2 = 7.39$, $df = 24$, $P = 0.999$) or among landscape types ($\chi^2 = 4.91$, $df = 24$, $P = 0.999$). Two thousand one hundred thirty-eight prey items were identified in White Stork diets within the study area, comprising 61 prey species distributed among 7 classes, 13 orders, 30 families and 54 genera. Twelve orders of prey were consumed in semi-arid colonies, and nine in both sub-humid and arid colonies. Invertebrate prey accounted for 95 % of all prey items, while vertebrate prey constituted the remainder. Insects were the most consumed prey for all climate zones (PF = 94 % of all prey items), of

Table 1 Dietary traits (*N*, PF, *B*) of prey species identified in white stork across a climate gradient in north-eastern Algeria

Class: order					Climate of white stork colonies						Overall		
		Sub-humid			Semi-arid			Arid					
Family	Species	*N*	PF (%)	*B* (%)	*N*	PF (%)	*B* (%)	*N*	PF (%)	*B* (%)	*N*	PF (%)	*B* (%)
Gastropoda: Stylommatophora ($S = 1$)		–	–	–	0.2	0.2	1.2	3	0.9	6.9	5	0.2	1.4
Helicidae	*Helix* spp. [20]	–	–	–	2	0.2	1.2	3	0.9	6.9	5	0.2	1.4
Arachnida: Araneae ($S = 1$)		5	0.6	<0.1	5	0.5	<0.1	1	0.3	<0.1	11	0.5	<0.1
Araneidae	Araneidae sp. [0.06]	5	0.6	<0.1	5	0.5	<0.1	1	0.3	<0.1	11	0.5	<0.1
Arachnida: Scorpionida ($S = 1$)		–	–	–	4	0.4	3.6	1	0.3	3.5	5	0.2	2.2
Buthidae	*Buthus occitanus* [30]	–	–	–	4	0.4	3.6	1	0.3	3.5	5	0.2	2.2
Insecta: Dermaptera ($S = 5$)		70	7.9	0.1	100	10.8	0.1	18	5.4	0.1	188	8.8	0.1
Anisolabididae	*Anisolabis mauritanicus* [0.05]	61	6.9	0.1	90	9.7	0.1	11	3.3	<0.1	162	7.6	0.1
Labiduridae	*Labidura riparia* [0.05]	3	0.3	<0.1	3	0.3	<0.1	1	0.3	<0.1	7	0.3	<0.1
Forficulidae	*Forficula auricularia* [0.05]	1	0.1	<0.1	4	0.4	<0.1	6	1.8	<0.1	11	0.5	<0.1
	Forficulidae sp. 1 [0.05]	5	0.6	<0.1	1	0.1	<0.1	–	–	–	6	0.3	<0.1
	Forficulidae sp. 2 [0.05]	–	–	–	2	0.2	<0.1	–	–	–	2	0.1	<0.1
Insecta: Blattodea ($S = 1$)		2	0.2	–	<0.1	–	–	–	–	–	2	0.1	<0.1
Blattidae	*Blatta* spp. [0.06]	2	0.2	<0.1	–	–	–	–	–	–	2	0.1	<0.1
Insecta: Orthoptera ($S = 5$)		31	3.5	3.9	28	3.0	1.5	14	4.2	6.4	73	3.4	3.0
Tettigoniidae	*Decticus* spp. [2.02]	7	0.8	0.5	1	0.1	0.1	–	–	–	8	0.4	0.2
Pamphagidae	*Pamphagus* spp. [4]	23	2.6	3.4	7	0.8	0.8	14	4.2	6.4	44	2.1	2.5
Gryllotalpidae	*Gryllotalpa gryllotalpa* [2.95]	–	–	–	2	0.2	0.2	–	–	–	2	0.1	0.1
Gryllidae	*Gryllus bimaculatus* [0.7]	1	0.1	<0.1	14	1.5	0.3	–	–	–	15	0.7	0.2
	Gryllus spp. [0.7]	–	–	–	4	0.4	0.1	–	–	–	4	0.2	<0.1
Insecta: Heteroptera ($S = 1$)		–	–	–	7	0.8	<0.1	–	–	–	7	0.3	<0.1
Lygaeidae	*Lygaeus* spp. [0.05]	–	–	–	7	0.8	<0.1	–	–	–	7	0.3	<0.1
Insecta: Coleoptera ($S = 35$)		727	82.6	8.7	723	78.0	6.9	278	84.0	7.9	1728	80.8	7.7
Carabidae	*Carabus* spp. [0.29]	6	0.7	0.1	5	0.5	<0.1	–	–	–	11	0.5	0.1
	Zabrus spp. [0.29]	1	0.1	<0.1	1	0.1	<0.1	–	–	–	2	0.1	<0.1
	Macrothorax morbillosus [0.29]	4	0.5	0.1	16	1.7	0.2	2	0.6	<0.1	22	1.0	0.1
	Scarites spp. [0.29]	4	0.5	0.1	1	0.1	<0.1	–	–	–	5	0.2	<0.1
	Calosoma spp. [0.29]	1	0.1	<0.1	1	0.1	<0.1	–	–	–	2	0.1	<0.1
	Feronia spp. [0.29]	1	0.1	<0.1	9	1.0	0.1	–	–	–	10	0.5	<0.1
	Chlaenius spp. [0.29]	20	2.3	0.2	36	3.9	0.3	9	2.7	0.3	65	3.0	0.3
	Campalita spp. [0.29]	18	2.0	0.2	19	2.1	0.2	2	0.6	<0.1	39	1.8	0.2
	Acinopus spp. [0.29]	143	16.3	1.5	135	14.6	1.2	41	12.4	1.4	319	14.9	1.3
	Licinus sp. [0.29]	1	<0.1	0.1	–	–	–	–	–	–	1	0.1	<0.1
Harpalidae	*Harpalus* spp. [0.2]	1	0.1	<0.1	3	0.3	<0.1	–	–	–	4	0.2	<0.1
	Harpalidae sp. [0.2]	2	0.2	<0.1	1	0.1	<0.1	1	0.3	<0.1	4	0.2	<0.1
Apionidae	*Apion spp. [0.1]*	7	0.8	<0.1	5	0.5	<0.1	–	–	–	12	0.6	<0.1
Silphidae	*Aclypea opaca* [0.1]	1	0.1	<0.1	4	0.4	<0.1	–	–	–	5	0.2	<0.1
	Silpha spp. [0.1]	48	5.5	0.4	68	7.3	0.4	19	5.8	0.4	135	6.3	0.4
	Necrodes spp. [0.2]	29	3.3	0.2	10	1.1	0.1	–	–	–	39	1.8	0.1
Staphylinidae	*Staphylinus* spp. [0.05]	18	2.0	<0.1	6	0.7	<0.1	1	0.3	<0.1	25	1.2	<0.1
Buprestidae	*Chrysobothris* spp. [0.2]	5	0.6	<0.1	7	0.8	<0.1	48	14.5	1.1	60	2.8	0.2
Geotrupidae	*Geotrupes* spp. [0.4]	159	18.1	2.3	138	14.9	1.6	6	1.8	0.2	303	14.2	1.7
Elateridae	*Athous* sp. [0.2]	1	0.1	<0.1	–	–	–	–	–	–	1	0.1	<0.1
Scarabaeidae	*Scarabaeus sacer* [0.5]	4	0.5	0.1	4	0.4	0.1	–	–	–	8	0.4	0.1
	Rhizotrogus spp. [0.5]	19	2.2	0.4	25	2.7	0.4	1	0.3	<0.1	45	2.1	0.3
	Onthophagus spp. [0.5]	18	2.0	0.3	7	0.8	0.1	1	0.3	<0.1	26	1.2	0.2
	Gymnopleurus spp. [0.5]	1	0.1	<0.1	4	0.4	0.1	–	–	–	5	0.2	<0.1
	Oryctes spp. [0.5]	1	0.1	<0.1	2	0.2	<0.1	–	–	–	3	0.1	<0.1
	Aphodius spp. [0.5]	34	3.9	0.6	44	4.8	0.7	2	0.6	0.1	80	3.7	0.6
	Bubas spp. [0.5]	12	1.4	0.2	3	0.3	<0.1	–	–	–	15	0.7	0.1
	Aethiessa floralis [0.5]	5	0.6	0.1	10	1.1	0.2	–	–	–	15	0.7	0.1
	Oxythyrea funesta [0.29]	31	3.5	0.3	40	4.3	0.4	34	10.3	1.1	105	4.9	0.4
Curculionidae	*Larinus* spp. [0.1]	11	1.2	0.1	19	2.1	0.1	2	0.6	<0.1	32	1.5	0.1
	Brachycerus spp. [0.01]	15	1.7	<0.1	34	3.7	<0.1	44	13.3	<0.1	93	4.4	<0.1
Cerambycidae	*Clytus* spp. [0.2]	7	0.8	0.1	6	0.7	<0.1	14	4.2	0.3	27	1.3	0.1
Tenebrionidae	*Pimelia* spp. [0.4]	85	9.7	1.2	42	4.5	0.5	44	13.3	2.0	171	8.0	1.0
	Blaps spp. [0.5]	11	1.2	0.2	16	1.7	0.2	–	–	–	27	1.3	0.2
	Timarcha spp. [0.5]	3	.3	0	0.1	2	<0.1	7	2.1	0.4	12	0.6	0.1
Insecta: Hymenoptera ($S = 1$)		1	0.1	<0.1	3	0.3	<0.1	3	0.9	<0.1	7	0.3	<0.1
Formicidae	*Messor Barbara* [0.001]	1	0.1	<0.1	3	0.3	<0.1	3	0.9	<0.1	7	0.3	<0.1
Amphibia: Anura ($S = 1$)		1	0.1	1.0	3	0.3	2.4	–	–	–	4	0.2	1.6
Ranidae	*Pelophylax saharicus* [27]	1	0.1	1.0	3	0.3	2.4	–	–	–	4	0.2	1.6
Reptilia: Testudines ($S = 1$)		–	–	–	1	0.1	1.8	–	–	–	1	0.1	0.9
Geoemydidae	*Mauremys leprosa* [60]	–	–	–	1	0.1	1.8	–	–	–	1	0.1	0.9

Table 1 (continued)

Class: order		Climate of white stork colonies									Overall		
		Sub-humid			Semi-arid			Arid					
Family	Species	*N*	PF (%)	*B* (%)	*N*	PF (%)	*B* (%)	*N*	PF (%)	*B* (%)	*N*	PF (%)	*B* (%)
Mammalia: Rodentia (*S* = 7)		19	2.2	16.6	22	2.4	13.5	6	1.8	11.1	47	2.2	14.4
Muridae	*Apodemus sylvaticus* [22.95]	3	0.3	2.5	–	–	–	–	–	–	3	0.1	1.0
	Apodemus sp. [22.95]	–	–	–	–	–	–	1	0.3	2.7	1	0.1	0.3
	Mus musculus [8]	–	–	–	5	0.5	1.2	–	–	–	5	0.2	0.6
	Mus spretus [10]	5	0.6	1.8	5	0.5	1.5	4	1.2	4.6	14	0.7	2.0
	Rattus norvegicus [28]	2	0.2	2.0	3	0.3	2.5	–	–	–	5	0.2	2.0
	Rattus spp. [33.2]	6	0.7	7.2	5	0.5	5.0	1	0.3	3.9	12	0.6	5.7
	Meriones shawi [28]	3	0.3	3.0	4	0.4	3.3	–	–	–	7	2.8	2.8
Aves: Galliformes (*S* = 1)		24	2.7	69.7	29	3.1	69.1	7	2.1	64.3	60	2.8	68.7
Phasianidae	Chicken remains [80]	24	2.7	69.7	29	3.1	69.1	7	2.1	64.3	60	2.8	68.7
All taxa (*S* = 61)		880	100	100	927	100	100	331	100	100	2,138	100	100

Estimated specific prey biomass in gramme is indicated in square brackets. Prey frequency (PF) refers to the proportion of *N* of each prey species to the total *N* per climate region

N, number of prey individuals; *B*, biomass; *S*, prey species richness

which the Coleoptera were the best represented, with 1,728 individuals (PF = 80.82 %, *S* = 35 species), followed by Dermaptera (PF = 8.79 %, *S* = 5 species) and Orthoptera (PF = 3.41 %, *S* = 5 species). Chicken remains were the most constant food item in the studied pellets. This food category also dominated dietary biomass (*B* = 68.97 %), followed by Rodentia (*B* = 14.41 %) and Coleoptera (*B* = 7.70 %; Table 1).

Dietary characteristics and food niche

The average number of prey items per pellet ranged between 30.1 ± 15.4 (mean ± standard deviation) in arid areas and 23.2 ± 14.4 in the semi-arid climate (where the maximum number of prey observed was 927, PF = 43 %). The highest value of species richness was recorded in semi-arid colonies, having 56 prey species (Sm = 7.7 ± 2.4 prey species per pellet) and in colonies located in rural and urban landscapes (both *S* = 54 prey species; Sm = 8.4 ± 3.0 and Sm = 8.2 ± 2.4, respectively), followed by 52 prey species for sub-humid colonies (Sm = 4.6 ± 5.6). Food niche breadth was broader in arid colonies (FNB/*S* = 0.36), although the highest values of FNB and *S* were recorded for semi-arid colonies (FNB/*S* = 0.25). Regarding prey species diversity and evenness, the diet of White Storks was more diversified in semi-arid and sub-humid climates (*H*′ = 4.5 and *H*′ = 4.3, respectively), compared to the arid climate sites (*H*′ = 3.9). Rural and urban colonies exhibited higher values of Shannon's index (*H*′ = 4.6 and *H*′ = 4.5, respectively), compared to suburban colonies (*H*′ = 3.6). Prey species were equally distributed under different climate types (evenness = 75.7–78.8 %), but they were slightly more evenly distributed in rural colonies (*E* = 79.7 %) compared to suburban colonies (*E* = 70.6 %) (Table 2).

Table 2 Variation of dietary parameters and food niche of White Stork across climatic and urbanization gradients in north-eastern Algeria

Diet parameters	Climate regions			Landscape types		
	Sub-humid	Semi-arid	Arid	Rural	Suburban	Urban
Number of individuals—*N*	880	927	331	805	337	996
Prey frequency—*PF* (%)	41.2	43.4	15.5	37.7	15.8	46.6
Mean *N* per pellet—Nm	24.4	23.2	30.1	21.8	24.1	27.7
Standard deviation of *N*	14.5	14.4	15.4	12.8	17.1	15.0
Species richness—*S*	52	56	30	54	33	54
Mean *S* per pellet—Sm	7.7	8.5	8.5	8.4	7.6	8.2
Standard deviation of *S*	2.4	2.8	2.4	3.0	2.3	2.4
Biomass (%)	39.5	48.1	12.5	44.6	17.9	37.5
Food Niche Breadth—*FNB*	11.8	14.0	10.7	14.8	6.6	14.9
Ratio FNB/*S*	0.23	0.25	0.36	0.27	0.20	0.28
Shannon index—*H*′	4.3	4.5	3.9	4.6	3.6	4.5
H′max	5.7	5.8	4.9	5.8	5.0	5.8
Evenness—*E* (%)	75.7	77.9	78.8	79.7	70.6	77.8

Table 3 Likelihood-ratio tests (LH) of the generalized linear models (GLMs) testing the effects of climates and landscape types on dietary parameters of White Stork populations breeding in north-eastern Algeria

Variables	*df*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
		Number of individuals		Biomass		Species richness		Food Niche Breadth	
Climate	2	10.4	0.06	0.9	0.63	1.1	0.59	2.2	0.33
Landscape	2	20.4	<0.01	2.9	0.23	0.2	0.89	0.4	0.84
Climate × landscape	1	1.6	0.21	1.8	0.18	0.3	0.56	0.2	0.70
		Ratio FNB/*S*		Shannon index		Shannon index max		Evenness	
Climate	2	1.1	0.59	2.4	0.31	1.4	0.50	1.7	0.43
Landscape	2	1.4	0.48	0.2	0.93	0.6	0.76	0.9	0.64
Climate × Landscape	1	0.1	0.84	0.3	0.59	0.3	0.60	0.3	0.61

LR test are *type II* because all predictor variables (climates and landscapes) are factors

df degrees of freedom

Variation of diet across climates and landscapes

The generalized linear model revealed that the number of prey individuals (*N*) varied significantly between climatic areas ($P = 0.01$) and between landscape types ($P < 0.01$). In addition, the GLMs showed that the remaining dietary parameters measured in each pellet did not vary significantly either between climates or between landscape types ($P > 0.05$). The effect of

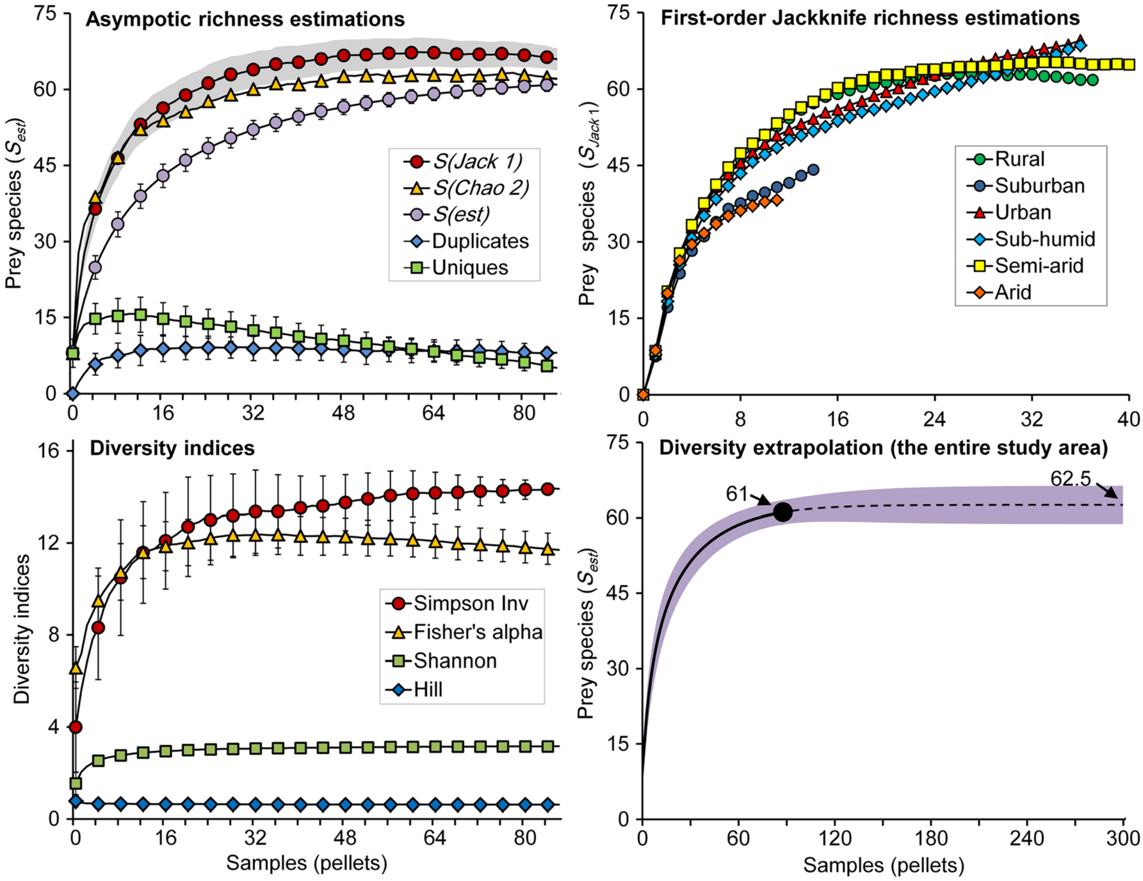


Fig. 2 Asymptotic richness estimation, diversity indices and rarefaction of prey species in White Stork diets in North Africa: *Top left*: sample-based rarefaction curves of three nonparametric richness estimators (analytical '$S_{(est)}$', first-order Jackknife '$S_{(Jack\ 1)}$' with SD represented by shaded area, and Chao 2 '$S_{(Chao\ 2)}$') and uniques 'Q_1' and duplicates 'Q_2' with SD as bars . *Bottom left*: diversity indices (Fisher's alpha, Shannon, Simpson and Hill) are given for the entire study area based on the reference sample of 87 pellets. Values represented in the curves are means with standard deviations (SD) as *vertical bars*. Only every fourth data point of the diversity indices and richness estimators are shown. Means and SD are computed based on 100 randomized sample 'runs' (see details in Colwell 2013). *Top right*: species richness estimated with the first-order Jackknife '$S_{(Jack\ 1)}$' for different climates and landscapes. *Bottom left*: rarefied and expected species richness for the whole study area. *Violet area* represents lower and upper bounds of 95 % confidence intervals (CI) for the analytical estimated species richness $S_{(est)}$

the interaction of these two factors (climate × landscape) on all dietary characteristics was not significant (Table 3).

Estimates of prey species richness

For the entire study area, i.e. all pellets pooled irrespective of the climatic region or landscape type, rarefaction curves increased slightly with the number of pellets before reaching a plateau (Fig. 2). Expected species richness curves calculated using the Chao 2 richness estimator '$S_{(\mathrm{Chao}\ 2)}$' and the first-order Jackknife richness estimator '$S_{(\mathrm{Jack}\ 1)}$' both proved to be stable and reached a plateau for the entire study area. Even though the shapes of the rarefaction curves for these two estimators are similar, $S_{(\mathrm{Jack}\ 1)}$ is probably the most appropriate for determining expected prey species richness in the White Stork diet. This is due to its correctness and robustness (Brose et al. 2003) and because its curve displayed higher values than that of $S_{(\mathrm{Chao}\ 2)}$. Moreover, this estimator presented an interval that covered all values of the estimated species richness generated with the other asymptotic estimators used in this analysis (Table 4).

Total prey species richness was estimated to be 66 prey species, while $S_{(\mathrm{Chao}\ 2)}$ indicated a value of 62 prey species for the White Stork diet (Fig. 2). The first-order Jackknife richness estimator revealed that the expected prey species richness in the diet decreased with increasing aridity. Total prey species richness was estimated to be 68.5 for sub-humid colonies, 64.8 for semi-arid colonies and 38.2 for the arid colony. Expected prey species richness was lower for colonies located in suburban landscapes with 44.1 prey species compared to urban and rural colonies where prey species richness was estimated to be 69.9 and 61.8, respectively (Table 4). Values for accumulated species, richness estimators, and diversity indices are reported in Table S5 (https://dx.doi.org/10.6084/m9.figshare.3463316) for each level of accumulation, from a single sampling unit to the full reference sample (per climate and landscape) up to a sampling size of 300.

Prey species richness extrapolations

Based on species richness extrapolation from the reference pellets of each climate zone and landscape to a theoretical sample size of 300 pellets, rarefaction curves revealed that the analytical species richness S_{est} kept increasing with the number of pellets in colonies located in urban and suburban landscapes and under sub-humid climates. S_{est} was expected to reach 95.5, 71.8 and 49.7 prey species in sub-humid climates, urban and suburban landscapes, respectively (Fig. 3). The prey species expected in semi-arid and arid climates, rural landscapes as well as in the entire study area reached a plateau, with S_{est} values expected for 300 pellets relatively close to those estimated for the reference sample of pellets. For 300 pellets, S_{est} was expected to be 62.5 prey species for the entire

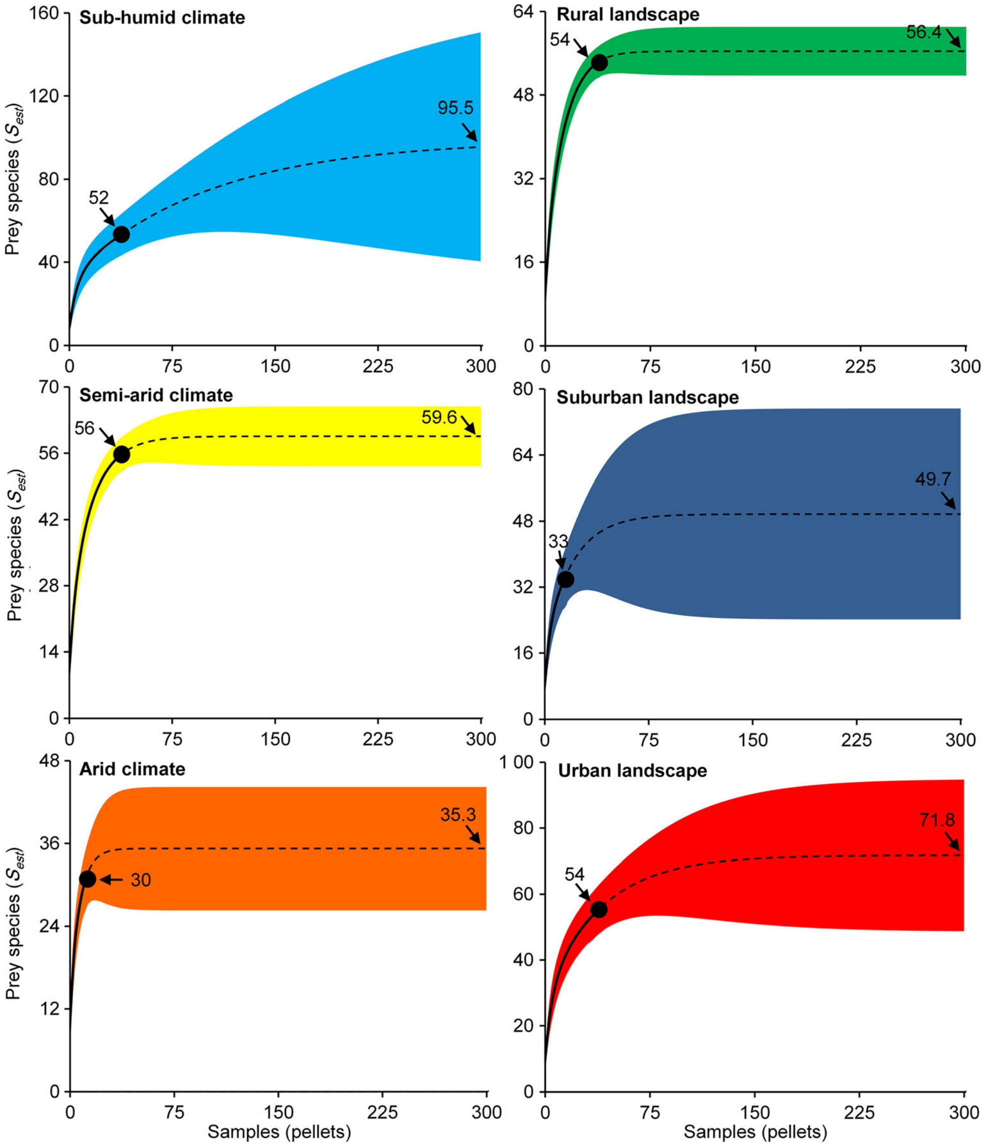
Table 4 Diversity indices and estimated total prey species richness for the diet of White Stork according to climate regions, landscape types, and the whole study area in North Africa

Diversity statistics	Climates of the colony			Landscapes of the colony			
	Sub-humid	Semi-arid	Arid	Rural	Suburban	Urban	Overall
Samples (pellets)	36	40	11	37	14	36	87
Individuals	880	927	330	805	337	996	2,138
S(est)	52	56	30	54	33	54	61
Singletons mean	13	7	9	5	11	14	4
Doubletons mean	3	5	4	6	2	5	5
Uniques mean	17	9	9	8	12	16	5
Duplicates mean	3	11	7	13	4	7	8
ACE mean	61.7	59.1	39.9	56.0	46.1	66.6	62.4
ICE mean	65.7	60.1	36.7	57.9	42.7	68.7	63.2
Chao 1 mean	71.5	59.5	37.2	55.4	51.3	69.2	62.0
Chao 2 mean	85.1	58.9	34.1	56.0	45.3	68.6	62.1
Jack 1 mean	68.5	64.8	38.2	61.8	44.1	69.6	65.9
Jack 2 mean	81.8	63.1	40.4	57.4	51.3	78.2	63.1
Bootstrap mean	58.9	61.1	34.0	59.0	38.0	60.9	64.3
MM runs mean	60.7	65.8	40.7	64.5	45.8	62.6	65.4
Coleman rarefaction	52	56	30	54	33	54	61
Alpha mean	12.1	13.1	8.0	13.1	9.1	12.2	11.7
Shannon mean	3.0	3.1	2.7	3.2	2.5	3.1	3.2
Simpson inverse mean	11.8	14.0	10.7	14.8	6.6	14.9	14.4
Hill mean	0.59	0.61	0.74	0.62	0.56	0.67	0.61

The diversity statistics are reported as analytically computed expected values, or as mean values averaged over 100 randomizations 'runs'. See Colwell (2013) for detailed description of species richness estimators and diversity statistics

ACE abundance coverage-based estimator, *ICE* incidence coverage-based estimator, *MM* Michaelis-Menten richness estimator

Fig. 3 Sample-based rarefaction and extrapolation curves of prey species richness estimated in the diets of White Storks along a gradient of climatic regions (sub-humid, semi-arid and arid) and urbanization landscapes (rural, suburban and urban) in North Africa. Reference pellet samples are indicated by *black solid circles*, rarefaction curves by *solid lines*, and extrapolation curves by dashed lines. *Coloured areas* represent lower and upper bounds of 95 % confidence intervals (CI) for the analytical estimated species richness $S_{(est)}$



study area, 59.6 and 35.3 prey species in semi-arid and arid climates, respectively, and 56.4 prey species in rural landscapes (Figs. 2 and 3). Table S5 (https://dx.doi.org/10.6084/m9.figshare.3463316) gives full diversity statistics including other species richness estimators and species diversity indices computed for climates, landscapes, and the total diet of White Storks in north-eastern Algeria based on the reference samples and extrapolated for a sample size of 300 regurgitated pellets.

Spatial similarities of the prey species

Prey species compositions assessed between the climatic regions and landscapes of the studied White Stork colonies indicated high similarity based on qualitative (Classic Jaccard and Sørensen similarity indices) or abundance-based indices. Among the climatic regions, all indices revealed that dietary similarity was highest between sub-humid and semi-arid colonies (Table 5). Considering landscapes, all indices showed the highest similarity in diet between rural and urban colonies. Both Chao's Jaccard and Chao's Sørensen indices applied using raw and estimated data showed the highest similarity values (>0.83) among climates and landscapes.

Discussion and conclusion

The White Stork is distributed across multiple habitats in north-eastern Algeria, where a remarkably steep climatic

Table 5 Spatial incidence-based (qualitative) and abundance-based similarities in White Stork diet between climates and landscapes of colonies

Spatial biodiversity similarity	Climate regions			Landscape types		
First colony sampled Second colony sampled	Sub-humid Semi-arid	Sub-humid Arid	Semi-arid Arid	Rural Suburban	Rural Urban	Suburban Urban
Observed *S* in first colony	52	52	56	54	54	33
Observed *S* in second colony	56	29	29	33	54	54
Shared species observed	48	26	28	31	48	30
Chao shared estimated	59.9	35.1	39.4	34.7	58.4	39.9
Classic Jaccard similarity index	0.80	0.47	0.49	0.55	0.80	0.53
Classic Sørensen similarity index	0.89	0.64	0.66	0.71	0.89	0.69
Raw Chao's Jaccard index	0.96	0.84	0.83	0.89	0.95	0.88
Estimated Chao's Jaccard index	1.00	0.92	0.89	1.00	1.00	1.00
Raw Chao's Sørensen index	0.98	0.91	0.91	0.94	0.97	0.93
Estimated Chao's Sørensen index	1.00	0.96	0.94	1.00	1.00	1.00
Morisita-Horn index	0.95	0.58	0.57	0.72	0.84	0.78
Bray-Curtis index	0.79	0.38	0.40	0.53	0.68	0.49

Chao's Jaccard and Chao's Sørensen indices are abundance-based indices (Chao et al. 2005)

gradient is prominent, but occurs mostly in humid, sub-humid and semi-arid areas. Some substantial colonies also exist under hot-arid climatic conditions (Si Bachir et al. 2013). My analysis of White Stork diet demonstrates that it feeds on larger and more diverse foods in sub-humid and semi-arid climatic conditions than in arid climates, as is also the case for urban landscapes compared to rural and suburban areas. This outcome could be explained by the greater availability of food resources in these areas. Arid regions are known as low productivity ecosystems due to their adverse ecological conditions that curtail the survival of many species (Noy-Meir 1973; Chenchouni 2012; Bradai et al. 2015).

Overall, dietary parameters were quite similar between sub-humid and semi-arid climates, as well as between colonies located in rural and urban landscapes. However, the White Stork seems to have a broader food niche under arid climates compared to sub-humid and semi-arid climates. This suggests that populations in arid zones expend more effort to attain their nutritional requirements (Ehrlich et al. 1993). Despite the diversity of prey species being low for arid climate colonies, the prey communities found in their diet showed higher values of evenness than those of the sub-humid and semi-arid areas. This reveals that the White Stork regularly consumes the same prey species in equivalent amounts in arid zones (and in rural landscapes), which is clearly shown in the tight confidence intervals for the extrapolation curves of prey species richness. In order to ensure a balanced diet under arid conditions, which is often synonymous with food shortages, birds need to increase foraging effort to match their nutritional needs, which can vary according to phenological breeding stages (Hilgartner et al. 2014; Chenchouni et al. 2015). This scenario is supported by *FNB* values, which are larger under arid conditions, representing clear evidence that generalist-foragers tend to expand their trophic niche under severe climatic conditions.

The observed differences in the frequencies of prey orders in diet across the studied climatic regions and landscapes may be explained by differences in foraging habitat productivities and food availability in these regions (Noy-Meir 1973). Certainly, arid areas are known to have lower primary productivity compared to mesic climatic areas (Bradai et al. 2015). So habitats under such conditions offer less abundant food resources, which forces birds to increase their feeding effort to attain the optimal diet.

Other studies investigating the dietary composition of the White Stork have indicated that it is an opportunistic forager (Peris 2003; Milchev et al. 2013). Two primary characteristics of its trophic niche are noteworthy: (1) in terms of consumed numbers of individuals, the diet is dominated by invertebrate prey (mainly coleopteran insects), with percentages exceeding 90 % of boli; and (2) in terms of biomass, these invertebrate prey represent only a small proportion of the total biomass so their energy contribution is marginal, with vertebrate prey contributing most energy (Barbraud and Barbraud 1998; Boukhemza 2001; Tsachalidis and Goutner 2002; Sbiki 2009; Vrezec 2009; Milchev et al. 2013). This opportunistic feeding behaviour explains the high values of dietary evenness (*E*), revealing that the White Stork is a dietary generalist *par excellence*.

This opportunism towards natural prey, as opposed to refuse scavenging, is more obvious for storks in arid climates that have a broader food niche breadth, indicating that they use the food resources of the foraging habitats in a complementary and compensatory manner to address their nutritional needs, impacting on fitness, reproductive performance and also migration outcomes (Drent et al. 2006; Byholm and Kekkonen 2008; van den Burg 2009; Hušek et al. 2013; Hilgartner et al. 2014; Djerdali et al. 2016). The GLMs revealed significant variation in the number of prey individuals, while other dietary parameters did not significantly differ, suggesting that the White Stork tends to balance its diet by ensuring a constant food supply whatever the climatic area or landscape type. The species achieves this balance by varying the numbers of consumed prey to match a constant biomass value, which results in a widening of its food niche breath by increasing its trophic niche in less productive areas/habitats or for periods of high food intake demand such as during pre- and post-migration and chick rearing.

Although insect prey represent only a small part of the dietary biomass, they are important for reproductive success, especially during the period of chick growth (Barbraud and Barbraud 1998). White Storks use insect prey when preferred prey (primarily vertebrates) are lacking in order to compensate and complement its food needs, particularly in hot-arid regions (Sekour et al. 2011). For quite similar reasons, chicken remains dominate the diet of the White Stork and constitute the major dietary biomass. White Storks consume chicken remains because they are constantly available, are abundant and are easily accessible in the uncontrolled trash dumps across North Africa. In addition, scavenging spares the White Stork as well as other bird species the effort of hunting down countless small prey of low calorific content. Therefore, the findings of this work indicate that urbanization level of colonies affects White Stork diet through intensive use of trash dumps as a food resource, which influences the productivity and numbers of breeding White Storks. This behaviour is not restricted to North African colonies (Chenchouni 2016), having been reported from European countries with mild climates such as Spain (Tortosa et al. 2002) and Poland (Kruszyk and Ciach 2010). In addition, the species can benefit from human socio-agricultural activities in North Africa, where agricultural development and rehabilitation of degraded arid lands is creating new favourable foraging habitats for White Storks (Johst et al. 2001; Latus and Kujawa 2005; Chenchouni 2016). However, agriculture intensification negatively affects bird productivity (Latus and Kujawa 2005; Tryjanowski et al. 2011; Janiszewski et al. 2014).

Scavenging from trash dumps is an increasingly common feeding strategy among several animal species, which usually select breeding and feeding habitats that are expected to provide perpetual abundant and available food of high quality and requiring low energy expenditure to acquire it (Alonso et al. 1991; Tortosa et al. 2002; Kosicki et al. 2006; Janiszewski et al. 2014). It is also possible that animal species frequently attend these man-made environments because natural environments do not always provide their food requirements, especially during periods of peak nutritional demand such as during brood rearing (Chenchouni et al. 2015; Djerdali et al. 2016), or during seasons of food scarcity occurring after severe climatic conditions or extreme weather events (Tryjanowski and Kuzniak 2002; Schaub et al. 2005; Tryjanowski et al. 2005a; Tryjanowski et al. 2009; Tobolka et al. 2015).

The White Stork also consumes other prey categories (such as Stylommatophora, Scorpionida, Blattodea, Heteroptera, Testudines) that are considered complementary to its diet, as they are found being consumed with low to moderate amounts on the one hand, and/or they are specific to a given climatic area on the other hand. In fact, the presence of some prey species in the diet and its composition in general depends on characteristics of the foraging habitats (Tryjanowski and Kuźniak 2002; Tsachalidis and Goutner 2002; Massemin-Challet et al. 2006).

As a synanthropic species, the diet of the White Stork is tightly linked to human activities. As a result, its bioecology and eco-ethology are significantly influenced and increasingly dependent on the resources and waste generated by humans and the habitat modifications due to diverse agricultural and urban activities (Chenchouni et al. 2016). Future studies of White Storks should investigate the effects of habitat modification and changes in land use (particularly urbanization and agricultural intensification) on food resources and breeding parameters (e.g. clutch size, chick survival and reproductive success), especially under arid conditions where habitats are less productive and the species is more reliant on anthropogenic food resources.

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Appendix

Table 6 Location, human population size, climatic and agricultural characteristics of study colonies of the White Stork in northeastern Algeria (North Africa)

	Sampled White Stork colonies							
	Merouana	Oued El Ma	K'sar Belezma	Seriana	Ferme Riche	Bouachaoune	Chemora	N'Gouas
Location and population								
Latitude (North)	35°41′39″	35°38′38″	35°40′31″	35°37′54″	35°40′04″	35°37′54″	35°37′22″	35°33′30″
Longitude (East)	6°11′02″	5°59′44″	5°08′81″	5°54′42″	6°22′23″	6°20′39″	6°17′32″	5°36′44″
Altitude (m)	931	1034	906	990	862	872	930	752
Surface area (km^2)	76.5	139.3	89.9	176.3	14.8	17.3	262.7	81.8
Population size (inhabitants)	41,125	15,434	9471	17,087	2931	3412	20,369	31,920
Climate variables								
Budyko radiation index of dryness	2.93	2.94	2.91	2.88	3.49	3.69	3.48	3.86
Budyko evaporation (mm/year)	410	410	409	402	344	332	344	319
Budyko runoff (mm/year)	17	17	18	16	9	8	9	6
Budyko evaporation (%)	95.9	95.9	95.8	96.1	97.5	97.7	97.5	98.2
Budyko runoff (%)	4.1	4.1	4.2	3.7	2.5	2.2	2.5	1.8
Aridity index	0.38	0.38	0.38	0.34	0.34	0.31	0.34	0.29
De Martonne index	19	19	19	17	15	14	15	14
Climatic NPP *	741	741	741	692	627	613	627	582
Precipitation (mm/year) **	367.7	387.7	371.4	366.1	324.0	322.0	344.3	269.9
Precipitation deficit (mm/year)	688	688	688	704	696	724	696	790
Gorczynski continentality index	37.4	37.1	37.2	36.3	28.6	30.4	28.3	40.4
Agricultural data (areas)								
Total agricultural surface (ha)	6000	4545	8600	12,000	957	1113	17,725	4800
Useful agricultural surface (ha)	5291	3837	8504	7602	794	924	16,098	4659
Irrigated agricultural surface (ha)	340	542	770	1709	15	17	240	695
Rangelands (ha)	290	426	70	1298	141	164	1000	141
Cereals (ha)	2850	3130	3142	4400	430	501	4630	700
Forage crops (ha)	277	276	484	1950	86	100	3250	500
Vegetable crops (ha)	221	171	356	517	2	2	18	23
Industrial crops (ha)	10	30	60	0	0	0	0	0
Arboricultural surface (ha)	59	31	34	36	33	38	115	545
Poultry data								
Meat broilers (chickens)	641,760	362,910	119,800	143,240	8090	9410	586,160	417,170
Egg-laying chickens (hens)	523,070	199,750	371,960	18,870	1330	1540	58,370	47,280

* NPP: net primary production in g of dry matter/m^2 /year, ** precipitation values refer to the year 2011

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