Ecology/Écologie

Patterns of resource partitioning by nesting herons and ibis: How are odonata exploited?

Modèles de partage de ressources par des hérons et ibis nicheurs : comment les odonates sont-ils exploités ?

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ABSTRACT

Herons and ibis are colonially nesting waders which, owing to their number, mobility and trophic role as top predators, play a key role in aquatic ecosystems. They are also good biological models to investigate interspecific competition between sympatric species and predation; two processes which structure ecological communities. Odonata are also numerous, diverse, mobile and can play an important role in aquatic ecosystems by serving as prey for herons and ibis. A relationship between prey size and bird predator has been observed in Numidia wetlands (NE Algeria) after analyzing food boluses regurgitated by six species of birds (Purple Heron, Black-crowned Night Heron, Glossy Ibis, Little Egret, Squacco Heron and Cattle Egret) during the breeding period, which also shows a temporal gradient for the six species. Both the Levins index and preliminary multivariate analysis of the Odonata as prey fed to nestling herons and ibis, indicated a high degree of resource overlap. However, a distinction of prey based on taxonomy (suborder and family) and developmental stage (larvae or adults) reveals a clear size dichotomy with large-sized predators (Purple Heron, Black-crowned Night Heron and Glossy Ibis) preying on large preys like Aeshnids and Libellulids and small-sized predators feeding mainly on small prey like Zygoptera. Overall, the resource utilization suggests a pattern of resource segregation by coexisting nesting herons and ibis based on the timing of reproduction, prey types, prey size and foraging microhabitats.

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RÉSUMÉ

Les hérons et les ibis sont des oiseaux d'eau coloniaux qui, grâce à leur nombre, mobilité et position dans les réseaux trophiques, jouent un rôle clé au sein des écosystèmes aquatiques. Ce sont également d'excellents modèles biologiques pour étudier la prédation et la compétition interspécifique entre espèces sympatriques, deux processus qui structurent les communautés écologiques. Les odonates sont également nombreux, divers, mobiles et ils peuvent remplir des rôles importants dans les écosystèmes aquatiques en servant de proies pour les hérons et ibis. Une relation entre taille de la proie et oiseau prédateur a été observée dans les zones humides de la Numidie (Algérie nord-orientale) après analyse des régurgitas

de six espèces d'oiseaux (Héron pourpré, Héron bihoreau, Ibis falcinelle, Aigrette garzette, Héron crabier et Héron garde-bœufs) lors de la période de reproduction, qui indique également un gradient temporel pour les espèces étudiées. L'indice de Levins et l'analyse multivariée ont tous deux indiqué un degré appréciable de chevauchement des ressources utilisées. Cependant, une distinction des proies basée sur la taxinomie (sous-ordre et famille) et les stages développementaux (larves ou adultes) indique une dichotomie nette de la taille qui distingue les prédateurs de grande taille (Héron pourpré, Héron bihoreau et Ibis falcinelle) prélevant les proies les plus larges comme les Aeshnidés et les Libellulidés alors que les prédateurs de petite taille se nourrissent de petites proies comme les Zygoptères. Globalement, l'utilisation des ressources suggère un modèle de ségrégation de ressources des hérons et ibis syntopiques basé sur le timing de la reproduction, le type et la taille de proies, et les microhabitats utilisés.

1. Introduction

Community ecologists have long sought to apprehend the various processes shaping coexistence and diversity and to distinguish the relative role of stochasticity and deterministic factors driving species' responses to environmental and spatio-temporal gradients [1–3]. A large amount of intensive effort focused on quantifying differences in resource use between species [4–6] as identifying resource exploitation patterns can indicate potential competitive interactions and provide information relevant to habitat management. When food is abundant, different bird species may coexist if no other limiting factors are present [7] but if resources are limited, interspecific competition between sympatric species and differences in their ability to exploit these resources can lead to resource partitioning through changes in diet, feeding behavior and spatio-temporal segregation [8,9]. Predator–prey relationships have also been the focus of much attention to interpret resource partitioning and niche distribution in ecosystems [10].

The study of the foraging ecology of sympatric wading birds and the extent of their segregation along niche axes has attracted considerable interest but this sustained effort has not achieved a consensus [11–17]. Water level is known to be a major factor regulating the abundances of aquatic birds and it may determine spatial segregation of bird species together with other factors like plant distribution and cover [18,19]. Information on the species' ecological requirements and community processes such as competition [20,21] and predation [22–24] is also useful for planning and ensuring the conservation and management of aquatic ecosystems [25].

In order to identify patterns of food use by wading birds and their relationships with respect to their distribution in wetlands, a study on diet components of six aquatic bird species was carried out in Numidia wetlands (NE Algeria) during the breeding season of 2003–2007, analyzing food characteristics and other behavior aspects. The objectives of this study are twofold: (1) document how odonata are used by breeding herons and ibis; (2) identify patterns of relationships between food and habitat use by aquatic birds.

2. Methods

Numidia, northeast Algeria, houses a large and diverse set of wetlands made up of freshwater shallow lakes, ponds, lagoons and brackish marshes [26,27]. The region encompasses a Biosphere Reserve, the El Kala National Park, Ramsar sites and numerous Important Bird Areas [28]. Numidia is also recognized as a national and regional hotspot for Odonata [29]. Between 2003 and 2007, we studied reproductive and diet characteristics of six species of herons, egrets and ibis: Cattle Egret (CE), *Ardea ibis* L.; Squacco Heron (SH), *Ardeola ralloides* Scop., Little Egret (LE) *Egretta garzetta* L., Black-crowned Night Heron (NH), *Nycticorax nycticorax* L., Purple Heron (PH), *Ardea purpurea* L. and Glossy Ibis (GI), *Plegadis falcinellus* L. during the breeding season [30–32].

Food boluses regurgitated by nestlings were collected across the wetland complex of Numidia, northeastern Algeria: Lake Tonga, Lake Fetzara, Dakhla, Chatt, Mekhada, Sidi Achour [28] between May and July during the years 2003–2006. Prey samples were kept in 70% ethanol and were later sorted and identified in the laboratory. Only the adults and larvae of the following broad taxonomic categories of the order Odonata: Zygoptera, Libellulidae and Aeshnidae, were considered in this study. Chicks of all species of herons and Glossy Ibis were individually marked, measured and weighed between 1–23 days [33]. To measure the degree of overlap of two utilization curves ($p_{x,i}$) and ($p_{y,i}$) (relative use of resource categories by each species), we used the Levins index [34]:

$$LO_{x,y} = \sum \left(\left(p_{x,i} \right) \left(p_{y,i} \right) \right) / \sum \left(p_{x,i} \right)^2$$

summed for all resource states i, with $p_{x,i}$ being the relative frequency of prey category i in the diet of species x or y and $LO_{x,y}$ the resource use overlap of species x with species y. The Levins index is asymmetric [the breadth of species y $(1/\sum (p_{y,i})^2)$ may differ from the breadth of species x $(1/\sum (p_{x,i})^2)$] and it ranges from 0 to slightly more than 1. Like most overlap indices, the Levins index does not account for differences in resource availability and must be used with care [35].

During March–April 2006 at Lake Tonga and Lake Oubeïra, one focal bird was chosen at random [36] and its foraging behavior (microhabitat, water level, number of steps, trials, successful catches, intra- and interspecific antagonistic behavior) was recorded for 15 minutes. Only interspecific behavior will be dealt with in this paper.

A data matrix (six species of birds/six categories of prey) was assembled and analysed using Principal

Component Analysis (PCA) with the ade4TkGUI package implemented in R [37,38].

3. Results

3.1. Breeding phenology

Despite a great variation and overlap in the timing of the reproduction of the six studied waders, a clear pattern still emerges with the Purple Heron nesting first followed by the Black-crowned Night Heron. The Little Egret and the Cattle Egret then follow with the Squacco Heron nesting last [33]. There is however a great amount of variability in the egg laying period exhibited by the studied herons and ibis. The length of the breeding period is linked to the number of asynchronous nucleii within a colony (Table 1). Egg laying for the Purple Heron is generally over by the end

of May whereas the Glossy Ibis has a somewhat protracted egg laying period stretching from mid-April to July [31,32].

3.2. Diet and interspecific antagonistic behavior

Odonata were incorporated frequently ($>25\%$) in the diet by five of the studied species and, for four of these, Odonata represented over 10% of prey items in their diet (Table 2). Size (energy content) seems to be relevant to prey consumption as Odonata larva were fed upon increasingly by more species as size increased (Fig. 1). In sharp contrast, Zygoptera (larva and adults) were mainly preyed upon by small-sized predators. High values of overlap of the utilization curves as measured by the Levins index were found between the larger species (Purple Heron, Black-crowned Night Heron and Glossy Ibis) and the smaller species (Squacco Heron, Little Egret and Cattle Egret), respectively (Table 3). Out of 20 interspecific

Table 1
Egg laying phenology of Purple Heron, Glossy Ibis and Squacco Heron in Numidia.

Species	Site and year	First egg date	Egg laying period (days)
Purple Heron	Tonga 2004	$<$ 14 April (several nucleii)	36
	Tonga 2005	31 March	45
	Dakhla 2006	31 March	35
	Fetzara 2006	5 April	N/A
Glossy Ibis	Tonga 2004	$\sim$ 15 April (several nucleii)	$\sim$ 75
	Tonga 2005	$\sim$ 10 May	$\sim$ 15
	Chatt 2007	23 April	N/A
	Fetzara 2007	30 May	N/A
Squacco Heron	Tonga 2004	9 May (several nucleii)	83
	Tonga 2005	2 May (two nucleii)	24
	Chatt 2006	5 May	20
	Fetzara 2006	19 May	23
	Dakhla 2007	7 May	38
	Fetzara 2007	16 May	25
Cattle Egret	Tonga 2004	21 April (several nucleii)	95
	Tonga 2005	25 April (two nucleii)	42
	Chatt 2006	25 April	22
	Fetzara 2006	14 May	28
	Fetzara 2007	15 May	25
Little Egret	Tonga 2004	24 April (several nucleii)	86
	Tonga 2005	28 April (two nucleii)	35
	Chatt 2006	28 April	20
	Fetzara 2006	15 May	22
	Fetzara 2007	16 May	23
Black-crowned Night Heron	Tonga 2004	8 May (several nucleii)	68
	Tonga 2005	20 April (two nucleii)	43
	Mekhada 2005	15 May	29
	Fetzara 2007	8 May	29

Table 2
Occurrence and number of Odonata prey items in the diet of herons and ibis nestlings' diet.

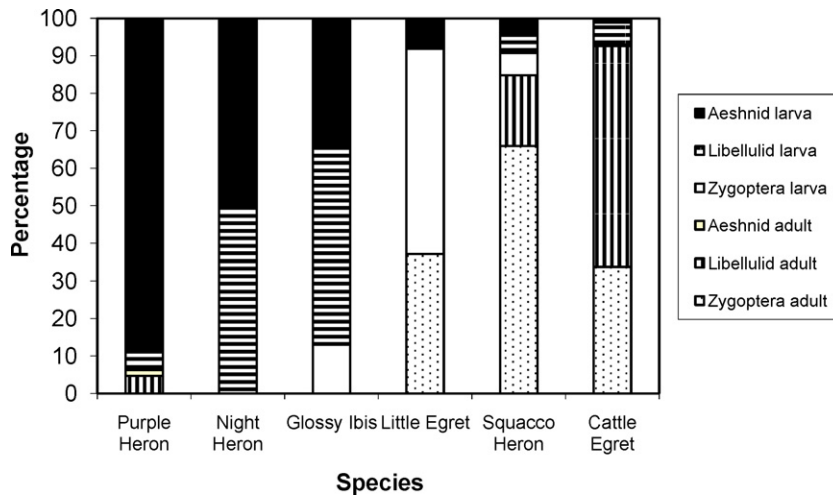|	Occurrence (%)	Number (%)	Food boluses	Prey items
Cattle Egret	27.8	5.0	243	4991
Little Egret	30.0	10.4	603	603
Squacco Heron	54.3	31.0	71	591
Black-crowned Night Heron	8.3	3.0	24	76
Glossy Ibis	42.1	13.0	21	169
Purple Heron	32.0	15.8	100	399

Fig. 1. Relative importance of Odonata in the diet of herons and ibis in their choice of Odonata.

agonistic encounters recorded, 11 involved the studied species, particularly the small-sized species: Squacco Heron, Little Egret and Cattle Egret (Table 4).

3.3. Multivariate analysis of diet

Despite some overlap in the use of prey species, results indicated a clear pattern of feeding segregation amongst nesting herons by their differential exploitation of different taxa or stages of Odonata which differ markedly in their size (biomass) and habitat use (Fig. 2). The factorial plane of the first two axes of the PCA (79% of inertia) revealed the structure of the data marked by a size dichotomy along the first axis between large species

(Purple Heron, Black-crowned Night Heron and Glossy Ibis) which prey on large preys like the Aeshnids and small predators which feed mainly on Zygoptera adults and larvae. The second axis reveals a gradient of habitat use from terrestrial to aquatic ones illustrated by Cattle Egrets that feed on adult Libellulids which can disperse far from water, Squacco Herons which mainly collect adult Zygoptera on the margins of ponds and lakes, and Little Egrets which wade in shallow water to prey on Zygoptera, both adults and larvae.

The third axis (16% of inertia) indicated that within the set of large predators, Purple Herons specialize on the largest preys, Aeshnid larvae, close to emergent vegetation, whereas Glossy Ibis feeds on Libellulid larvae in more open

Table 3
Levins index for overlap of herons and ibis in Numidia based on odonata as prey. Data correspond to overlap of species on each row with species on the columns.

Species	Purple Heron	Night Heron	Little Egret	Squacco Heron	Cattle Egret	Glossy Ibis
Purple Heron	1	0.59	0.09	0.06	0.18	0.42
Night Heron	0.94	1	0.08	0.09	0.07	0.87
Little Egret	0.16	0.09	1	0.63	0.28	0.22
Squacco Heron	0.09	0.10	0.59	1	0.71	0.1
Cattle Egret	0.32	0.08	0.27	0.73	1	0.08
Glossy Ibis	0.82	1.06	0.24	0.12	0.08	1

Table 4
Number of recorded interspecific agonistic encounters between different species of herons and ibis.

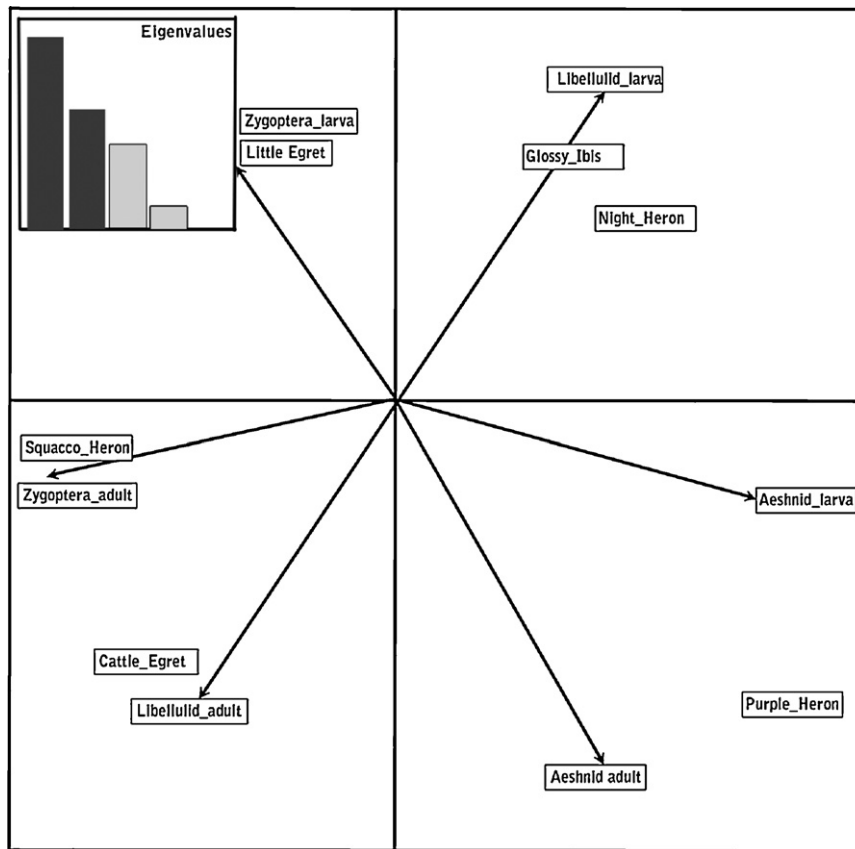| Species	GE	LE	GH	WS	CE	PH	SH	NH	GI	Total
Great Egret (GE)										0
Little Egret (LE)										0
Grey Heron (GH)	5	2								7
White Stork (WS)				1						1
Cattle Egret (CE)		1								1
Purple Heron (PH)										0
Squacco Heron (SH)		5	1		3					9
Black-crowned Night Heron (NH)										0
Glossy Ibis (GI)					2					2
Total	5	8	2	0	5	0	0	0	0	20

Fig. 2. Biplot of factorial plane 1 × 2 of PCA of the food of herons and ibis' nestlings. Eigenvalues are provided in the insert.

habitats (Fig. 3). The limited data on the nocturnal Black-crowned Night Heron suggest a diet intermediate between the latter two species. The fourth axis (5% of inertia), separated the Squacco Heron which feeds more on adult Zygoptera from the Little Egret which specializes on larval Zygoptera.

4. Discussion

Reproductive success is tightly linked to foraging success [39]. In two seminal papers [40,41], Hutchinson described the degree of limiting similarity among coexisting, congeneric species based on morphological character divergence. Hutchinson's rule predicts that species that differ sufficiently in size or life history traits, may also differ in resource use to avoid competitive exclusion. The rule also implies that niches of herons and ibis in Numidia are spaced in a non-random way in Hutchinson's hypervolume with minimal overlap in at least some dimensions [4,42,43]. The link between niche overlap and competition can be fairly complex [44] and much theoretical and experimental effort has been devoted to finding mechanisms explaining coexistence of competing species [5,45]. Resource competition is acknowledged as one of the most important processes that structure ecological communities [46] and, likewise, predation is also widely accepted as a major structuring force that may

affect prey populations by influencing behavior and habitat use [47,48]. A greater knowledge of resource competition and predation as well as mechanisms underlying these important processes and their interplay is required for the conservation of vanishing colonial waterbirds in a water-stressed region facing global changes [49].

The reproductive period is a critical period in the birds annual life cycle, when trophic resources may be limited and geared to meet the specific needs of developing chicks [50]. Resource competition at this stage may affect vital rates (e.g. birth and survival) and influence population dynamics. However, interspecific competition is relaxed through differences in the timing of reproduction of sympatric species which staggers to some extent the peak of energy demands of developing chicks [51]. Temporal partitioning may thus facilitate coexistence between competitors in ecological communities [52,53]. The studied species (both prey and predators) show a sequential distribution of their breeding time in accordance with similar observations of the same species in other geographic zones [54–56]. Chick development is closely linked to chick provisioning which in turn is linked to food availability and rate of parental provisioning [57,58]. Diel temporal partitioning may also mediate coexistence between predators and prey but the detailed diurnal time budget of local herons and ibis deserves
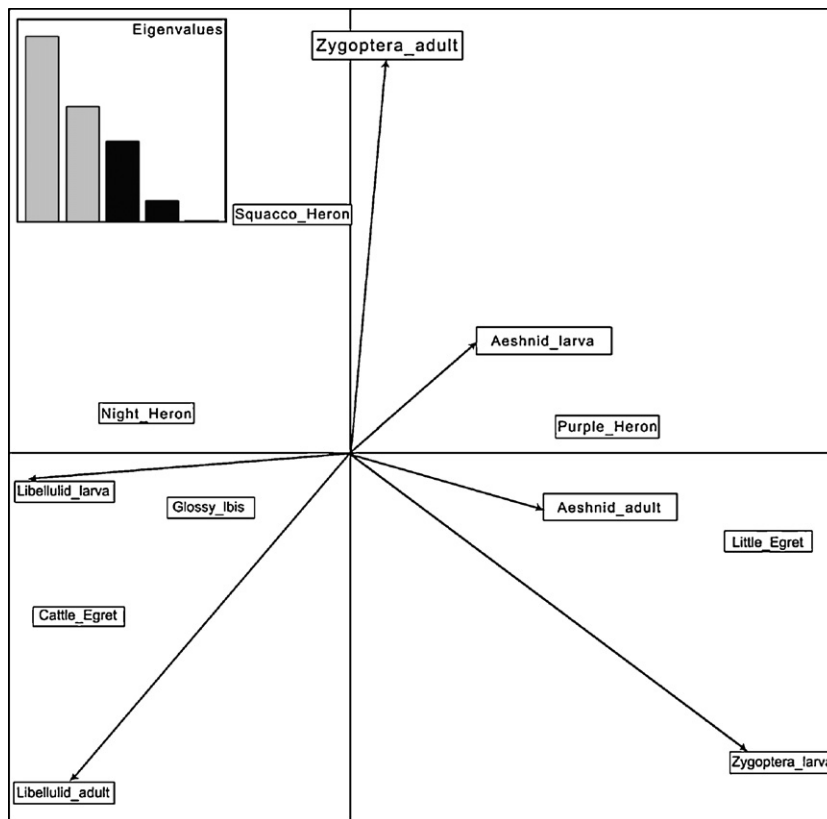
Fig. 3. Biplot of factorial plane 3 × 4 of PCA of the food of herons and ibis' nestlings. Eigenvalues are provided in the insert.

further investigation. In the study area, the Black-crowned Night Heron is the only nocturnal wader although diurnal foraging is carried out by breeding pairs at the height of the reproductive season [59]. Perhaps, significantly, the emergence of Aeshnids, a time of high vulnerability, is carried out before dawn, at a time when most avian predators are inactive. Both Aeshnids and Libellulids, which are also strong flyers, are highly vulnerable when flying in tandem during copulation and egg laying.

Another way to lessen competition between the studied herons and ibis is through the use of a wide range of feeding methods, probably aimed at distinct types of prey [39]. Purple Herons uses the 'stand and wait' [51,60] in relatively deep waters to capture prey (odonata, fish and other taxa) too large for any other heron and ibis to handle and, as expected from the analysis of his diet, this large heron hardly interacts with smaller-sized waders. The Glossy ibis forages in groups by probing the substrate in shallow waters and although, like the Black-crowned Night Heron, it preferentially incorporates Libellulid larvae in its diet, it can hardly be considered a strong competitor to a mainly piscivorous guild. Antagonistic interactions have been noted between the Glossy Ibis and Cattle Egret when the two overlap in the same microhabitat (wet open pastures). Direct interference competition seems to be concentrated mainly among the small body-sized set (Little Egret, Cattle Egret and Squacco Heron) with high overlap of their utilization curves. This is especially true for

the Little Egret and the Squacco Heron which also share other prey (Mosquito Fish *Gambusia holbrooki* Girard and amphibians) and which exhibit the highest rate of aggressive interactions. The former uses relatively deep waters and adopts diverse and most active feeding techniques to capture Zygopteran larvae, small fish, crustacea and amphibians. In contrast, the latter favors slow paces along the shallow parts of the shore of wetlands or waits motionless for prey to pass by before striking. This differential use of microhabitats and feeding strategies may help partition resources between the two species as has been found in other wading bird communities [61]. The last species, Cattle Egret, is mainly a terrestrial insect specialist which favors flying odonata which it hunts around dryer margins of waterbodies. Some scattered observations carried out at Lake Tonga and other neighboring wetlands corroborate this as they reveal that the studied species occupy distinct microhabitats with the Cattle Egret foraging mainly on wet and dry pasture lands adjacent to waterbodies; the Squacco Heron is generally found on the margin of wetlands and on floating vegetation within the waterbodies; the most active wader, the Little Egret, forages in shallow, open waters whereas the Purple Heron favors deeper parts in the littoral zone close to reed beds and other emergent vegetation; and the Glossy Ibis is found in wet pastures and open shallow areas whereas the Black-crowned Night Heron, which rarely forages during the day, has been recorded on the banks of canals.

Predators preferentially hunt prey of an optimal size in order to maximize the net rate of energy intake. Hence, prey body size is a trait that has been well documented to play a large role in influencing predator's choice [62,63] and capture of distinct prey length, correlated with the body size of herons, may be one way to achieve resource partitioning [64–66]. However, a positive relation between size of herons and size of prey may not be decisive in niche segregation [67]. In Numidia, size of odonata but also of fish prey (unpub.) varies within the large waders set (Purple Heron, Black-crowned Night Heron and Glossy Ibis) and within that of the small waders set (Little Egret, Cattle Egret and Squacco Heron).

Diet overlap amongst local waders is lessened by resource use of distinct predators on different prey or developmental stages based on body size and habitat use. However, because of the dynamic properties of the niche, more information is needed about resource partitioning by the studied waders when resource levels are reduced and competition heightened [68,69]. The differential exploitation of Odonata may be the result of habitat selection of both prey and predators and further research is needed to explore the spatial distribution of Odonata. Resource partitioning through the differential use of foraging areas and distinct antagonistic behavior deserves further study [61,70,71].

Odonata, at least in numbers, form a sizeable component of the diet of nestling herons and ibis in Numidia, northeast Algeria as elsewhere [72,73] and their utilization suggests a pattern of resource partitioning by nesting herons and ibis similar to that found in southern Florida [12] and Australia [74], but future studies should examine how other taxa (fish, amphibians, etc.) are exploited and attempt to disentangle various interacting processes that shape the composition of ecological communities.

Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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