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Seasonal diet of the Grey Heron *Ardea cinerea* on an oceanic island (Tenerife, Canary Islands): indirect interaction with wild seed plants

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Abstract. In 199 pellets analyzed a total of 7 460 prey items were counted, 96.2% of which were arthropods. Aeshnidae larvae (Odonata) made up 66.1% of the total prey items and were the main invertebrate group. Vertebrates constituted 3.8%, with reptiles and mammals being the main prey of this type (1.8% each). Despite the small size of the invertebrates, this group reached > 60% in terms of biomass. All the main prey items varied significantly among seasons. Odonata was the most important group in all seasons, reaching its maximum value in summer. In the case of vertebrates, reptiles were captured mainly in spring, mammals in winter. With regard to indirect interaction with seeds, a total of 901 seeds associated with lizard remains were found in 77 pellets, indicating that they had previously been consumed by these reptiles. External visual damage of seeds was low and only 1.1% was destroyed. No seeds germinated after the four-month germination experiment and practically all of them were unviable. In conclusion, these results indicate that Grey Heron diet on islands varies in comparison with continental zones, including an important number of invertebrates and reptiles. Furthermore, this bird acts as an opportunistic secondary seed disperser, although its ecological effect does not seem to be very significant for the dynamics of the Canary Island ecosystems.

Key words: Grey Heron, *Ardea cinerea*, feeding ecology, seasonal diet pattern, secondary seed disperser, islands

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INTRODUCTION

The Grey Heron is mainly a winter visitor in the Macaronesian archipelagos (Snow & Perrins 1998), although recent breeding records have been mentioned in the Cape Verde Islands (Palacios & Barone 2001). In the Canaries, only some unsuccessful nesting attempts have been recorded (Martín & Lorenzo 2001). In these islands (e.g. Tenerife) some individuals are present throughout the year, not only using inland reservoirs as feeding sites, but also fields, water sources in ravines and xeric flat lands. Its winter population ranges between 29–62 individuals (Martín & Lorenzo 2001).

Grey Heron diet, during the breeding season, has been well documented in Europe by using several methods (Owen 1955, Hewson & Hancox 1979, Giles 1981, Moser 1986, Draulans et al. 1987, Marquiss & Leitch 1990, Peris et al. 1995, Lekuona & Campos 1998, Jakubas & Mioduszewska 2005). However, information on its seasonal feeding habits throughout the year remains scarce, probably because in the northern part of its geographical range the species shows a migratory behaviour. Furthermore, very little is known about the feeding ecology of this heron in insular environments, particularly in oceanic islands (Voisin 1991, Sawara et al. 1994, Nanpo & Matsuda 2006).

In general, the Grey Heron shows piscivorous feeding behaviour in continental ecosystems. Nevertheless, preliminary observations carried out in the Canaries have shown that most of the pellets have a high content in Odonata larvae and, less frequently, aquatic beetles (Martín & Lorenzo

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2001). Furthermore, this heron preys upon lizards in the Canarian archipelago. In this regard, the consumption of fleshy fruits and subsequent seed dispersal process by lizards is a relatively common finding in tropical and subtropical oceanic island ecosystems (see Olesen & Valido 2003 and references therein). This framework suggests that herons could be functioning as secondary seed dispersers of some native plants in the Canary Islands, as occurs with other bird species (Nogales et al. 1998, 2002). However, the ecological significance of this interaction depends greatly on the secondary disperser. Data contained in the two scientific contributions previously cited demonstrate how the Southern Grey Shrike *Lanius meridionalis* is a legitimate disperser for *Lycium intricatum* (Solanaceae) and how the Kestrel *Falco tinnunculus* is an illegitimate disperser of their seeds. One of the main factors that explain these results is the fact that gut enzymatic action is clearly stronger in the diurnal raptor. Furthermore, it is also interesting to note that this ecological interaction depends on the seed coat thickness of the plant species which is participating in the interaction. With regard to the Grey Heron and its digestive seed treatment, it is important to note that its gut enzymatic action is rather strong (Hibbert-Ware 1940, Vinokurov 1960), causing degradation in most of the prey items appearing in the pellets. Thus, it would be very interesting to perform experiments on the viability and ability to germination of the seeds found in heron pellets as a result of its predation on frugivorous lizards.

In the present study, pellets were used to determine the annual Grey Heron diet in one of the most important roosting sites in Tenerife Island (Martín & Lorenzo 2001). This method was selected because it is able to supply a representative sample size (see Methods). Three main aims of this study are: 1) to describe, in detail, the seasonal variation of the Grey Heron diet in an oceanic island environment; 2) to compare these insular trophic patterns with those of different continental populations; and 3) to assess the ecological interaction with wild seed plants from the Canary Islands.

STUDY AREA AND METHODS

The material was collected in the Valle Molina water reservoir (Tegueste), located in the northeast of Tenerife Island (Canarian Archipelago, 27°37′–29°25′N and 13°20′–29°25′W). This locality is situated at 340 m a.s.l. and is surrounded by different types of crops (mainly vines), grassland zones and villages. The climate is subtropical and oceanic, this area receiving around 400–500 mm of mean annual rainfall and having a mean annual temperature ranging between 16–19°C (Marzol 2000).

This reservoir has a maximum area of 7.5 ha and has a perimeter of 1034 m. Its bottom is covered by a plastic layer and its banks have not been colonized by plants. Grey Herons use this place as a roosting site and foraging area. Other heron species such as the Little Egret *Egretta garzetta* and the Cattle Egret *Bubulcus ibis* are regularly present at this place, in addition to many migratory species (ducks, waders, gulls, etc.) (see Martín & Lorenzo 2001). While the pellets were collected (see details in the following section), two-monthly censuses were carried out to assess a minimum size of the study population. A mean of 14.2 ± 7.3 (max and min values = 33 and 1 individuals, respectively) Grey Herons were counted. A mean sighting of 14.2 individuals throughout the year would represent a range of 22.9–48.9% with respect to the total population estimated in Tenerife by Martín & Lorenzo (2001).

Collection, quantification and methodological considerations on pellets

At the beginning of each month throughout 2004, all the margins of the reservoir were cleared, removing or destroying all pellets found, to ensure that only fresh pellets were collected. A minimum of twenty pellets were collected, when possible, at the middle and at the end of each month (two visits per month), but they were seasonally grouped. A total of 60 pellets were gathered in spring and summer, but only 48 and 31 in winter and autumn, respectively. Each pellet was wrapped in aluminium foil, stored in a plastic bag and dried at room temperature prior to analysis.
All pellets were broken up by hand under dry conditions, after which different items were separated. Invertebrate remains were identified using a stereo-microscope (8× magnification) (Baéz 1985, Ralph et al. 1985). Some doubtful prey remains were identified by referring to the collection of the Zoology Department (University of La Laguna). The minimum number of individuals present in each pellet was estimated according to the most commonly found body parts, which represented one individual (heads, mandibles, legs, sclerotized parts, caudal appendages, etc.).

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Invertebrates less than 1 cm long were not considered in this study because these items occurred in association with reptilian remains ($G_1 = 96.61$, $p < 0.001$). In the case of Oligocheates, due to their soft body, only frequency of occurrence was recorded. In the case of mammal remains, teeth, lower jaws and bones contributed to the identification of some prey items. Since the majority of Grey Heron pellets do not contain these parts (Hibbert-Ware 1940, Draulans et al. 1987, Marquiss & Leitch 1990), mammalian fur samples were identified by comparison with a previously prepared reference collection, and also by using the identification keys developed by Day (1966). From each pellet, ten hairs were sampled for microscopic analysis, following the same protocol used by Jakubas & Mioduszewska (2005). We assumed that a minimum of one mammalian specimen was eaten by a heron when the species occurred in a pellet, following the Amat & Herrera (1978) criteria for other species. In some instances, fish and reptilian remains were mainly identified on the basis of their respective scale traits.

Data on diet are presented in four ways: number of prey items (NP), prey item percentage (%P, the number of items of a particular prey taxon recorded in the diet as a percentage of the total number of prey items identified), percentage frequency of occurrence (%FO, the percentage of pellets containing a particular prey taxon), and percentage contribution to dietary biomass (%B). Wet biomass was calculated using an average weight for reptiles (personal data) and mean weights for mammals and birds were obtained from the literature (Castells & Mayo 1993, Cramp 1998). In the case of the main arthropods and fish, we collected several individuals (five at least) of each identified taxon and took their fresh weight using an electronic balance (precision: 0.01 g).

Several techniques (direct observations, analysis of stomach contents, food regurgitated by nestlings at nest, or undigested remains from regurgitated pellets) have been used to determine Grey Heron diet, but all of them present some degree of bias (see Marquiss & Leitch 1990). The absence of breeding colonies in the Canaries (Martín & Lorenzo 2001) limited us to using prey remnants or chick regurgitation in heronries. Only a small sample of stomach contents from dead birds could be obtained because their corpses are difficult to find. Furthermore, direct observations of herons at their feeding sites was greatly hindered by their erratic feeding habits (van Vessem et al. 1984, pers. obs.), and the notable diversity of feeding sites identified in a small area in Tenerife. All the above, together with the presence of an accessible communal roosting site, where herons are present throughout the year, forced us to use pellet analysis. However, this method presents a degree of bias based on the differential digestion rate of each prey item (Milstein et al. 1970, Draulans et al. 1987, Marquiss & Leitch 1990). In this sense, fish and amphibians are almost absent in pellets, and mammal quantification is also difficult because of the almost complete lack of key bones (Milstein et al. 1970, Draulans et al. 1987, Marquiss & Leitch 1990).

Ingested seeds, germination and status

All seeds found inside pellets were preserved in a dry, dark place until they were identified using the reference collection of the IPNA-CSIC, at La Laguna. Most of them (n = 753) were planted separately in a 4 cm^2 pot, using a standard substrate (50% culture soil, 25% turf and 25% volcanic sand). To control environmental conditions, a germination experiment was performed in a greenhouse located at Tagoro (Tenerife: 300 m a.s.l.), a locality near (4 km) to the study area where pellets were collected. Therefore, night-day light period conditions were the same as those naturally found at the study site. Each seed was buried about 5 mm deep and watered every two days over four months (December 2005 – March 2006). Data were recorded every five days.

Due to the relatively small number of seeds found in the heron pellets, we decided to plant the majority of the samples. To assess the apparent status of embryos, a sub-sample of seeds (n = 129) of the main represented plants (n = 7 species) that did not germinate during these four months were extracted from the soil and then observed by using a stereo-microscope (8–50× magnification).

Statistical and index analysis

To study seasonal variation of the main items found in the diet, likelihood ratio tests were applied directly to the number of prey items which appeared in the pellets. These analyses compared a certain prey item with the total number of the remaining prey items identified. In those cases where it was necessary to use the same data set, this statistical effect was reduced by applying a more conservative sequential Bonferroni technique, for assessing statistical significance (Rice 1989). Due to the scarce presence of some prey items (Aranea, Tricoptera, Mantodea, Lepidoptera, Pisces, etc.), it was not feasible to

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carry out any statistical inference. Diet similarity or overlap among the different seasons was evaluated using the Morisita index of similarity for percentage of prey, whose values near "0" indicate low similarity and values near "1", a high similarity. Moreover, niche-breadth was assessed using the standardized Levin's niche-breadth index, where values close to "0" indicate dietary specialization and values close to "1", a broad diet (Krebs 1989). To calculate the index values, we used the taxonomical level of order for invertebrates and species for vertebrates. Since it was impossible to assign numbers for Oligochaetes, this prey item was not included in the index analyses.

To test whether or not seeds of fleshy fruits in pellets occurred in association with lizard remains, their presence in each pellet was recorded individually and a likelihood ratio test was used to assess such an association. All analyses were performed by using SPSS (version 12.0).

RESULTS

General diet composition

A total of 7 460 prey items were identified in the 199 pellets analysed, 96.2% corresponding to arthropods and the remainder consisting mainly of vertebrates (Table 1). A high variety of insect families was recorded. Aeshnidae larvae (Odonata), representing 66.1% of the total prey items, was the main invertebrate group. This family was followed in number by Libellulidae larvae (Odonata, 23.8%), Acrididae (Orthoptera, 1.3%) and Carabidae (Coleoptera, 1.1%). With regard to the vertebrates (3.8% of the total prey items), the principal groups corresponded to reptiles and mammals (1.8%, respectively).

In terms of FO, invertebrates clearly predominated in the diet (94.0%); specifically, Aeshnidae was the most important family (59.8%). The next most frequent groups were Acrididae (18.6%), Libellulidae larvae (15.6%), Gryllidae (9.1%), and Carcinophoridae (Dermaptera) and Hymenoptera (7%, respectively). Furthermore, Oligochaetes occurred at 1.1% of pellets and vertebrates at 68.8% of FO. In this case, mammals (53.8%) and reptiles (48.4%) were the most relevant groups (Table 1).

As for biomass, despite the low size of invertebrates in comparison with vertebrates, the most important group was Odonata (61.4%), Aeshnidae (57.3%) being the main family represented (Fig. 1). Introduced mammals (mice, rats, shrews and rabbits) constituted the second group in importance (27.4%) followed by reptiles (8.9%). Fishes, amphibians and birds were negligible prey items for the total biomass.

Seasonal variation in diet

All the main prey items varied significantly among seasons. Odonata was the most important group in all seasons although its consumption varied significantly, being highest during the summer ($G_3 = 54.19$, $p < 0.001$). The two main groups of this order were Aeshnidae and Libellulidae larvae. The former larvae showed statistical significance among seasons ($G_3 = 10.45$, $p = 0.015$), but their consumption was lower in summer. Seasonal variation was also observed in the case of Libellulidae ($G_3 = 844.24$, $p < 0.001$), but they were more frequently captured during summer. The maximum peak of grasshoppers was observed in autumn ($G_3 = 255.53$, $p < 0.001$). Acrididae were most frequently eaten in winter and spring, while the diet in autumn was characterised by the presence of Tettigonidae and Gryllidae. The consumption of Dermaptera (Carcinophoridae) reached maximum values in spring and winter ($G_3 = 102.20$, $p < 0.001$). With regard to vertebrates, reptiles appeared more often in spring ($G_3 = 156.43$, $p < 0.001$), mammals in winter ($G_3 = 129.54$, $p < 0.001$) and fish in autumn. 70.1% of total mammals corresponded to House Mice *Mus domesticus* which characterised the diet in autumn ($G_3 = 87.51$, $p < 0.001$). Other groups, such as fish, shrews, rabbits, and the

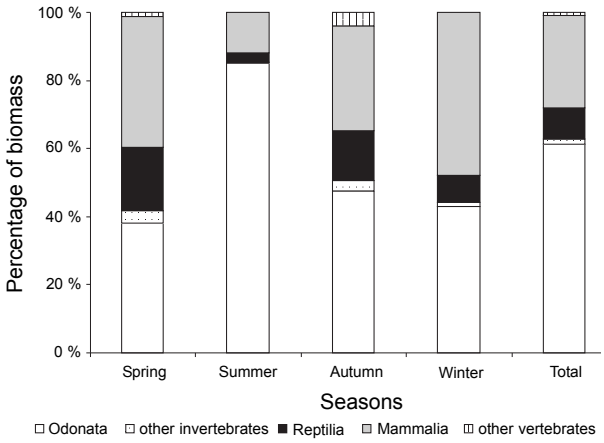


Fig. 1. Percentage of wet biomass for each group of prey items consumed by the Grey Heron on Tenerife (Canary Islands) in different seasons.

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Table 1. Seasonal changes in diet composition in the Grey Heron (January 2004–December 2004) on Tenerife (Canary Islands). Numbers in brackets correspond to pellets analysed. NP — number of prey items, %P — percentage of prey, % FO — frequency of occurrence in pellets.

Prey items	Spring (N = 60)			Summer (N = 60)			Autumn (N = 31)			Winter (N = 48)			Total (N = 199)		
	NP	%P	%FO	NP	%P	%FO	NP	%P	%FO	NP	%P	%FO	NP	%P	%FO
Invertebrates	990	89.4	98.3	4654	99.2	100	556	90.4	87.1	975	93.3	85.4	7175	96.2	94.0
Oligochaeta	-	-	31.7	-	-	-	-	-	-	-	-	6.3	-	-	11.1
Araneae	3	0.3	3.3	0	0	0	3	0.5	6.5	4	0.4	6.3	10	0.1	3.5
Diplopoda	7	0.6	1.7	0	0	0	0	0	0	0	0	0	7	0.1	0.5
Odonata	767	69.3	58.3	4583	97.7	93.3	479	77.9	51.6	895	85.6	62.5	6724	90.1	68.8
Orthoptera	63	5.7	28.3	16	0.3	13.3	64	10.4	51.6	39	3.7	33.3	182	2.4	28.6
Dermaptera	24	2.2	21.7	0	0	0	0	0	0	17	1.6	2.1	41	0.5	7.0
Tricoptera	2	0.2	1.7	2	0	3.3	6	1.0	3.2	0	0	0	10	0.1	2.0
Mantodea	0	0	0	0	0	0	1	0.2	3.2	1	0.1	2.1	2	0	1.0
Hemiptera	7	0.6	8.3	32	0.7	3.3	0	0	0	6	0.6	4.2	45	0.6	4.5
Coleoptera	106	9.6	31.7	6	0.1	8.3	2	0.3	6.5	11	1.1	12.5	125	1.7	16.1
Lepidoptera	7	0.6	8.3	1	0	1.7	0	0	0	0	0	0	8	0.1	3.0
Hymenoptera	5	0.5	8.3	10	0.2	11.7	1	0.2	3.2	2	0.2	2.1	18	0.2	7.0
Hexapoda indet.	0	0	0	2	0	3.3	0	0	0	0	0	0	2	0	1.0
Vertebrata	117	10.6	76.7	39	0.8	41.7	59	9.6	80.7	70	6.7	72.9	285	3.8	68.8
Pisces	6	0.6	5.0	1	0	1.7	7	1.1	3.2	0	0	0	14	0.2	2.5
Gambusia affinis	5	0.5	3.3	1	0	1.7	7	1.1	3.2	0	0	0	13	0.2	2.0
Gen. sp. indet.	1	0.1	1.7	0	0	0	0	0	0	0	0	0	1	0	0.5
Amphibia	1	0.1	1.7	0	0	0	0	0	0	0	0	0	1	0	0.5
Rana perezi	1	0.1	1.7	0	0	0	0	0	0	0	0	0	1	0	0.5
Reptilia	66	6.0	70.0	18	0.4	25.0	26	4.2	58.1	25	2.4	43.8	135	1.8	48.4
Gallotia galloti	32	2.9	51.7	12	0.3	20	12	2.0	38.7	11	1.1	22.9	67	0.9	33.2
Chalcides viridanus	34	3.1	56.7	6	0.1	10	14	2.3	45.2	14	1.3	29.2	68	0.9	34.2
Aves	0	0	0	0	0	0	1	0.2	3.2	0	0	0	1	0	0.5
Calidris sp.	0	0	0	0	0	0	1	0.2	3.2	0	0	0	1	0	0.5
Mammalia	44	4.0	56.7	20	0.4	26.7	25	4.1	67.7	45	4.3	75.0	134	1.8	53.8
Mus domesticus	29	2.6	48.3	15	0.3	25.0	20	3.3	64.5	30	2.9	62.5	94	1.3	47.2
Rattus sp.	12	1.1	20.0	3	0.1	5.0	2	0.3	6.5	9	0.9	18.8	26	0.3	13.1
Suncus etruscus	3	0.3	5.0	1	0	1.7	3	0.5	9.7	5	0.5	10.4	12	0.2	6.0
Oryctolagus cuninculus	0	0	0	1	0	1.7	0	0	0	1	0.1	2.1	2	0	1.0
Total of prey	1107			4693			615			1045			7460		

invertebrates (Lepidoptera or Hymenoptera) appeared in small numbers (Table 1). Oligochaetes occurred in two seasons, spring (31.7% of FO) and winter (6.3%).

In terms of biomass, Odonata were the most important dietary component in summer (85.1%), when mammals and reptiles decreased in numbers. In spring and winter, the most relevant group was mammals (38.3% and 47.9%, respectively). Reptiles attained their maximum value in spring (18.7%) (Fig. 1).

Levin's niche breadth (B) was broader in spring (0.063) and narrower in summer (0.003). In the other two seasons this index had medium values (autumn = 0.047 and winter = 0.025). The Morisita index indicates a high trophic overlap throughout practically all seasons, spring and summer showing the clearest differences in values with respect to the other two seasons (Table 2).

Indirect seed interaction

A total of 901 seeds were counted in all analysed pellets. Seeds from at least 12 taxa were identified at species level, representing 90.5%. After extraction from pellets, external visual damage of seeds ingested by the Grey Heron was low (1.1%) (Table 3). No seeds germinated after the four month experiment. Data on embryo viability indicate that only 4.7% seeds could still be alive after the germination experiment, indicating that the Grey Heron digestive gut effect caused significant damage to seed fate (Table 4). Seeds present in pellets were significantly associated with the presence of lizard remains ($G_1 = 75.96$, $p < 0.001$), which indicates that these seeds were previously consumed by these reptiles and indirectly by the herons.

DISCUSSION

Composition diet and seasonal variation

This study provides the first detailed description of the seasonal variation through a year of the Grey Heron diet on an oceanic island. However, the majority of contributions in continental ecosystems were made during the breeding period (Owen 1955, 1960, Hewson & Hancox 1979, Giles 1981, Moser 1986, Marquiss & Leitch 1990, Peris et al. 1994, 1995, Lekuona & Campos 1998, Lekuona 1999, 2001, Jakubas & Mioduszewska 2005).

Differences in diet composition between continental and insular areas were found (Table 5). It has been suggested that the diet varies considerably according to different habitats and seasons, and the studied species exhibits opportunistic feeding behaviour (Voisin 1991, Fasola et al. 1993, Cramp 1998). In the Canaries, Grey Herons often feed at agricultural ponds, but the physical characteristics of the majority of these reservoirs, which are usually deep with steep high banks, hinder fish capture (Draulans 1987, Voisin 1991). On marine shores, other species of fishes are available, but unlike more northern latitudes (Lekuona 1999, Carss & Elston 2003), the Grey Heron practically does not use this habitat as a foraging site in Tenerife (pers. obs.). Therefore, the low number of fish recorded in the present study may be due to limited access. On the other hand, it was found that the bulk of the diet in Tenerife was composed of Odonata larvae, which are present at both of these sites and in addition to all manner of natural bodies of water (Malmqvist et al. 1995), and may be more accessible than fish to herons because they remain relatively still near the surface on the pond walls until ready to leave the water. This prey item has been poorly represented in several studies carried out in Europe (Hibbert-Ware 1940, Draulans et al. 1987, Campos 1990, Jakubas & Mioduszewska 2005). Reptiles are rarely consumed in continental areas (Hibbert-Ware 1940, Moser 1986, Campos 1990, Peris et al. 1994, 1995, Cramp 1998, Jakubas & Mioduszewska 2005) but in Tenerife they constitute almost 50% of FO. This phenomenon may be related to the high density of lizards in insular environments (Olesen & Valido 2003, and references therein). In other predatory vertebrates studied in the Canaries, the same pattern was recorded (Carrillo et al. 1994, Nogales & Medina 1996, Padilla et al. 2005). Furthermore, contrary to other studies carried out in continental environments (Cuesta et al. 1980, Campos 1990, Peris et al. 1995, Jakubas & Mioduszewska 2005), invertebrates constituted more than 50% of ingested biomass. However, this result is probably a consequence of the

Table 2. Morisita's niche overlap index for Grey Heron diet between seasons in Tenerife (Canary Islands); results are based on percentage of prey for each food item.

Seasons	Summer	Autumn	Winter
Spring	0.934	0.983	0.972
Summer	-	0.967	0.990
Autumn	-	-	0.992
Winter	-	-	-

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Table 3. Seeds found in Grey Heron pellets over a year (January–December 2004) on Tenerife (Canary Islands). N — number of pellets, NS — number of seed, %S — percentage of seeds, %FO — frequency of seed occurrence in pellets, %DS — percentage of seeds visually damaged. Nomenclature of plant species follows the check-list of Izquierdo et al. (2004).

Plant species	Family	Spring (N = 60)		Summer (N = 60)		Autumn (N = 31)		Winter (N = 48)		Total (N = 199)			
		NS	%S	NS	%S	NS	%S	NS	%S	NS	%S	%FO	% DS
Solanum cf. *nigrum*	Solanaceae	216	40.3	38	53.5	3	1.4	2	2.4	259	28.7	5.0	-
Atriplex semibaccata	Chenopodiaceae	97	18.1	1	1.4	27	12.8	37	44.0	162	18.0	6.5	-
Rubus ulmifolius	Rosaceae	1	0.2	1	1.4	135	64.3	2	2.4	139	15.4	2.5	2.2
Lycopersicon esculentum	Solanaceae	111	20.7	8	11.3	-	-	-	-	119	13.2	3.5	-
Rubia fruticosa	Rubiaceae	47	8.8	-	-	-	-	1	1.2	48	5.3	3.5	-
Opuntia maxima	Cactaceae	-	-	8	11.3	34	16.2	-	-	42	4.7	2.5	4.8
Canarina canariensis	Campanulaceae	13	2.4	-	-	-	-	-	-	13	1.5	0.5	-
Lantana camara	Verbenaceae	-	-	-	-	-	-	13	15.5	13	1.5	1.0	-
Jasminum odoratissimum	Oleaceae	9	1.7	-	-	-	-	-	-	9	1.0	0.5	-
Teline sp.	Fabaceae	6	1.1	-	-	-	-	3	3.6	9	1.0	2.0	-
Chenopodium sp.	Chenopodiaceae	3	0.6	1	1.4	5	2.4	-	-	9	1.0	2.0	-
Vitis vinifera	Vitaceae	-	-	7	9.9	1	0.5	-	-	8	0.9	2.0	-
Avena sp.	Poaceae	2	0.4	1	1.4	-	-	-	-	3	0.3	1.0	-
Malva parviflora	Malvaceae	2	0.4	-	-	-	-	-	-	2	0.2	1.0	-
Achyranthes aspera	Amaranthaceae	1	0.2	-	-	-	-	-	-	1	0.1	0.5	-
Unidentified seeds	-	28	5.3	6	8.4	5	2.4	26	30.9	65	7.2	8.7	21.7
Total		536		71		210		84		901		38.7	1.1

impossibility to quantify mammals (only one individual was assumed to be present in each pellet). All these findings seem to indicate that differences in Grey Heron diet (mainland vs. islands) are based on distinct availability of potential prey items in foraging areas.

In our study area, seasonal variation of diet was high and all main prey items identified varied significantly. The consumption of vertebrates (reptiles and mammals) clearly decreases in summer, when lizards are more abundant and most active. However, this pattern was observed in mammalian prey in other studies performed during the breeding season (Campos 1990). In contrast, peak consumption of Odonata larvae occurs in summer. Dragonfly larvae are present throughout the year in the Canaries, but their demographic explosion takes place in spring and summer (Báez 1985), which would explain vertebrate prey substitution by Odonata larvae. This change in predatory behaviour is probably based on the greater availability of these prey.

The highest value obtained from Levin's niche breadth in spring is a result of an increase of insect abundance after autumn and winter rains. Due to the high abundance of Odonata larvae (Báez 1985) and the fact that herons concentrate their predation on certain prey components (Müller 1984), the niche breadth index decreases to a minimum during the dry season. Considering the mild climate throughout the year in this archipelago (Marzol 2000), and the low diversity of prey on islands, the important trophic niche overlap explains the high diet similarity recorded among seasons.

Seed interaction

Six of 12 plant species identified in seed analyses (*Solanum* cf. *nigrum*, *Rubus ulmifolius*, *Rubia fruticosa*, *Canarina canariensis*, *Jasminum odoratissium* and *Malva parviflora*) were native and the remainder corresponded to species introduced by man (see Izquierdo et al. 2004). One species from the former group (*R. fruticosa*) is endemic to the Macaronesian Islands and another (*C. canariensis*) is endemic to the Canarian Archipelago. However, these species together constituted only 6.8% of the total seeds indirectly ingested by the Grey Heron. Furthermore, 57.7% of the total identified seeds corresponded to native species, while a total of 42.3% were from introduced plants.

No germination and visual embryo analysis indicate that the digestive treatments, particularly the strong gut enzymatic effect on seeds in herons

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Table 4. Seed status and germination of the different species indirectly consumed by the Grey Heron on Tenerife (Canary Islands).

Plant species	Number of seeds planted	% germinated seeds	Number of seeds extracted after germination	% apparent viable seeds
Solanum cf. *nigrum*	230	0	-	-
Rubus ulmifolius	135	0	24	12.5
Atriplex semibaccata	130	0	14	0
Lycopersicon esculentum	95	0	19	0
Rubia fruticosa	47	0	21	0
Opuntia maxima	38	0	30	10
Gen. sp. indet.	19	0	-	-
Canarina canariensis	13	0	-	-
Lantana camara	13	0	13	0
Jasminum odoratissimum	9	0	8	0
Unidentified seeds	24	0	-	-
Total	753	0	129	4.7

(Hibbert-Ware 1940, Vinokurov 1960) produce a clear negative effect on all plant species. In contrast seeds from the majority of these species, passed through a lizard gut, presented a considerable germination rate (Nogales et al. 2005, Authors' unpublished data). This negative effect on *L. intricatum* seeds, when the secondary disperser shows a strong enzymatic action, has been observed in other birds, such as some diurnal raptors (Nogales et al. 2002). However, when the second seed interaction is carried out by non-specialised predatory birds (e.g. the Southern Grey Shrike) the fate of the seeds is clearly different in terms of viability and germination (Nogales et al. 1998). Furthermore, another negative ecological effect caused by herons, in the majority of seeds, is that they concentrate great numbers of seeds in their roosting sites. These places, mainly located on the margins of reservoirs and coastal cliffs, are not suitable micro sites for seed germination and seedling establishment.

Comparing seed number and frequency of occurrence per plant species in Grey Heron pellets with those of other birds (e.g. kestrels and shrikes), the incidence was found to be higher in the latter because their predation on lizards is more frequent (see Nogales et al. 1998, 2002) and thus the interaction with wild seeds is more probable. Lastly, with the increasing knowledge of trophic interactions in subtropical islands, such as the Canarian Archipelago, it can be seen that the participation of predatory birds (e.g. herons, diurnal and nocturnal raptors, shrikes, etc.), as legitimate/illegitimate secondary seed dispersers, is a more common phenomenon than it has been thought to be. The intervention of Grey Heron as an illegitimate secondary seed disperser is a rather novel ecological interaction for this species. However, considering the relatively low number of seeds that occurred in pellets in comparison with the millions of seeds annually dispersed by abundant endemic lizards and passerines, the role of herons does not seem to be of great significance in the dynamics of Canarian ecosystems.

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Table 5. Differences in Grey Heron diet composition, according to different sites and methods. RF — regurgitated food, GC — gut contents, DO — direct observations, PL — pellets, * — values lesser than 0.1, † — values referred to percentage of prey, § — values referred to frequency of occurrence.

Method	Locality	Main prey groups						Source
		Invertebrates	Fish	Amphibians	Reptiles	Birds	Mammals	
RF	England	26.9	70.9	0.2	0	0.1	1.9	Owen 1955 †
	England	26.4	71.4	0.1	0	0.1	2	Owen 1960 †
	Southeast France	17.6	81.9	0.3	0.1	0	0.1	Moser 1986 †
	Northern Italy	10.7	50.0	4.8	7.1	0	1.2	Fasola et al. 1993 †
	Japan	15.9	76.4	7.3	0	0	0.4	Sawara et al. 1994 †
	Northern Poland	?	95	1.2	0	0	0.9	Jakubas & Mioduszewska 2005 †
GC	Northern Italy	68.3	26	21	24	0	12.5	Moltoni 1936 in Cramp 1998 §
	Spain	44.4	55.5	0	0	0	11.1	Bernis & Valverde 1954 §
	Hungary	25.1	40.1	20.3	0	0	14.5	Vasvari 1954 in Cramp 1998 †
	Germany	44	53	1	0	0	2	Schlegel 1964 †
	Central and Western Spain	53.7	40.8	1.1	1.1	?	2.5	Cuesta et al. 1980 †
	Switzerland	78	73	0	0	0	45	Müller 1984 §
	Northeast Spain	44.4	55.6	0	0	0	0	González-Martín & González-Solís 1990 †
DO	Southwest France	17.5	82.1	0.4	0	0	0	Lekuona 1999 †
	Northern Spain	21.0	73.1	2.8	1.2	0	1.8	Lekuona 2001 †
RF & PL	Scotland	12.1	35.4	12.9	0	0	39.6	Giles 1981 †
	Scotland	1.6	69.5	0.8	0	21.1	7.0	Marquiss & Leitch 1990 †
RF, GC & PL	Central-West Spain	11.9	81.6	0.6	0.8	0.8	4.2	Campos 1990 †
	Central-West Spain	14.1–20.0	62.9	1.8	0.6	1.5	3.2	Peris et al. 1995 §
PL	England	?	0	0	0	30.0	75.0	Milstein et al. 1970 §
	Northeast Scotland	38.9	0	0	0	29.6	98.1	Hewson & Hancox 1979 §
	Northern Poland	26–51	1-5	0.2–0.3	0	0.5–0.9	99.9	Jakubas & Mioduszewska 2005 §
	Tenerife, Canary Islands	96.2	0.2	*	1.8	*	1.8	Present study †

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STRESZCZENIE

[Pokarm czapli siwej na Teneryfie (Wyspy Kanaryjskie) w cyklu rocznym — pośrednie związki z rozsiewaniem nasion].

Na Teneryfie nie istnieje lęgowa populacja czapli siwej, choć osobniki tego gatunku obserwowane są na tej wyspie przez cały rok. Pokarm ptaków określano analizując wypluwki zbierane na brzegach dużego zbiornika wodnego wykorzystywanego przez ptaki jako miejsce żerowania i noclegu. Łącznie zebrano 199 wypluwek, w których stwierdzono 7 460 okazów zdobyczy, wśród których 96,2% stanowiły stawonogi. Wśród bezkręgowców dominowały larwy ważek z rodziny żagnicowanych (Aeshnidae), które stanowiły do 66.1% wszystkich zdobyczy. Kręgowce, głownie ssaki i gady stanowiły tylko 3.8% zdobyczy (Tab.1). Zaobserwowano dość znaczne zmiany sezonowe w składzie pokarmu (Fig. 1, Tab. 2). Ważki były najważniejszym pokarmem przez cały rok, a ich największy udział w diecie zanotowano latem. Wśród kręgowców ssaki łapane były najczęściej zimą, zaś gady — wiosną.

Łącznie w wypluwkach znaleziono 901 nasion 12 taksonów (Tab. 3). Obecność nasion związana była z pozostałościami po skonsumowanych jaszczurkach, co wskazywałoby, że zostały one wcześniej zjedzone przez te gady. Zewnętrznie nasiona te nie były prawie uszkodzone. Jednakże żadne z nich nie skiełkowało w okresie czterech miesięcy po zasadzeniu, co wskazuje, że straciły żywotność po przejściu przez system trawienny czapli (Tab. 4). Wydaje się więc, że w związku z żerowaniem na jaszczurkach ptaki biorą udział w rozsiewaniu nasion, choć ich rola w tym procesie nie jest istotna w ekosystemie wysp Kanaryjskich.

W pracy zestawiono także dane o pokarmie czapli siwej zebrane w wielu miejscach i różnymi metodami (Tab. 5).

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