Bird Study

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tbis20

An investigation of the insect component in the diet of the Grey Heron *Ardea cinerea* and Little Egret *Egretta garzetta*

Emily Wilkinson, Robert B. Angus, Maxwell V. L. Barclay, Roger G. Booth, Anthony C. Galsworthy & David Morritt

To cite this article: Emily Wilkinson, Robert B. Angus, Maxwell V. L. Barclay, Roger G. Booth, Anthony C. Galsworthy & David Morritt (21 Aug 2024): An investigation of the insect component in the diet of the Grey Heron *Ardea cinerea* and Little Egret *Egretta garzetta*, Bird Study, DOI: 10.1080/00063657.2024.2386863

To link to this article: https://doi.org/10.1080/00063657.2024.2386863

© 2024 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group

Published online: 21 Aug 2024.

Submit your article to this journal

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=tbis20

BIRD STUDY
https://doi.org/10.1080/00063657.2024.2386863

OPEN ACCESS Check for updates

An investigation of the insect component in the diet of the Grey Heron *Ardea cinerea* and Little Egret *Egretta garzetta*

Emily Wilkinson[a], Robert B. Angus[a,b], Maxwell V. L. Barclay [b], Roger G. Booth[b], Anthony C. Galsworthy[b] and David Morritt[a]

[a]Department of Biological Sciences, Royal Holloway University of London, Egham, UK; [b]Insects Division, The Natural History Museum, London, UK

ABSTRACT

Capsule: Aquatic insects made up a relatively small part of the Grey Heron's diet, while Little Egrets consumed numerous beetles, both aquatic and terrestrial.

Aims: To explore the extent of insect predation by Grey Herons and Little Egrets. Regurgitated pellets were collected from beneath trees in which herons and egrets were nesting.

Methods: Seventy Grey Heron and 48 Little Egret pellets were collected from the RSPB reserve at Northward Hill, Kent. These pellets were disaggregated and prey items were collected and sorted under a binocular microscope.

Results: Grey Herons fed on a relatively small number of aquatic beetles (Coleoptera: seven species, 32 individuals) and bugs (Hemiptera: two species, six individuals). Little Egrets, in contrast, fed on a diverse array of beetle species, both aquatic (three families, 11 species, 48 individuals) and terrestrial (10 families, 35 species, 111 individuals), and also a few aquatic bugs (one family, one species, three individuals). The extent of terrestrial beetles in the diet constitutes new information for Little Egrets.

Conclusion: Insects, both terrestrial and aquatic, represent an important component of the diet of Little Egrets. For Grey Herons, insects are a very minor component of the diet, involving aquatic species only.

ARTICLE HISTORY
Received 14 June 2023
Accepted 9 July 2024

There are five species of heron (Ardeidae) that regularly breed in the UK, including the Grey Heron *Ardea cinerea* and Eurasian Bittern *Botaurus stellaris*, with three species being relatively recent additions to the breeding avifauna (Little Egret *Egretta garzetta*, Cattle Egret *Bubulcus ibis* and Great White Egret *Ardea alba*). Although heron species are typically associated with wetlands, they forage in both aquatic and terrestrial habitats, and so have a varied diet. Dietary studies are relatively scarce, however, particularly for the recently colonizing egret species. Such information is useful in assessing the species' conservation needs, as well as aiding the identification of possible conflicts with fisheries or agriculture.

Initial accounts of the diet of the Grey Heron and Little Egret are summarized by Cramp *et al.* (1977). A detailed analysis of the diet of the Grey Heron in Poland is given by Jakubas & Mioduszewska (2005). Based on analysis of regurgitated pellets from three Grey Heron colonies, they found that the pellets contained mammal hair (almost 100% of samples) and bones (20–24%), mainly from the European Water Vole *Arvicola amphibius* and *Microtus* spp. voles, and invertebrate remains (26–51%), mainly from the Great Diving Beetle *Dytiscus marginalis*. In two of the colonies, however, fish accounted for more than 95% of the regurgitated prey items. Marquiss & Leitch (1990), working on heron colonies by Loch Leven, in Scotland, noted that the herons were preying on ducklings as well as some other waterbird chicks, and also mentioned Great Diving Beetles as occasional prey items. It may also be noted that the Great Diving Beetle was recorded as a significant component of the summer diet of Grey Herons in West Stirlingshire, Scotland (Giles, 1981).

Included among the prey items of Grey Herons found by Jakubas & Mioduszewska (2005) were two specimens of the tiny (3.5–4.5 mm) whirligig beetle

CONTACT Robert B. Angus r.angus@rhul.ac.uk Department of Biological Sciences, Royal Holloway University of London, Egham, UK Insects Division, The Natural History Museum, London, UK

© 2024 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group
This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (http://creativecommons.org/licenses/by-nc-nd/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

Gyrinus minutus and one of the small (3.9–5.3 mm) diving beetles *Hyphydrus ovatus*. Also included were a few terrestrial beetles: 10 ladybirds (Coccinellidae), five leaf beetles (Chrysomelidae), and a few others. Moltoni (1936) found that in northern Italy the frequency of insects in the summer diet amounted to 68.3%. These included adults and larvae of hydrophilid and dytiscid water beetles, as well as dragonflies (Odonata) and terrestrial mole-crickets *Gryllotalpa*.

The diet of Little Egrets in France was studied by Valverde (1956), and in Russia by Dimentiev & Gladkov (1951). Valverde found that in the Camargue the egrets consumed a total of 31 unidentified adult Coleoptera as well larger larvae (length 50–80 mm) of *Dytiscus* and Hydrophilidae, with smaller (1ength 22–35 mm) Hydrophilidae and *Cybister* (Dytiscidae) species also represented. Valverde (1956) also recorded Little Egrets eating small unidentified dragonfly larvae, and four specimens of the terrestrial mole-cricket *Gryllotalpa*, the only terrestrial insect recorded in that study. Dimentiev & Gladkov (1951) found that, while in the winter the birds fed almost exclusively on fish, in summer they also ate various aquatic insects and their larvae, with large numbers of Orthoptera (grasshoppers, locusts, and crickets), dragonflies and their larvae. In the second half of the summer terrestrial insects were particularly often found in the stomachs of investigated birds.

The habitat preferences and foraging areas of Grey Herons and Little Egrets in the River Frome area of Dorset (England) were studied by Wood & Stillman (2014), at a time when the egret had only recently begun to colonize Britain. They found that the habitat preference and utilization of the two species were broadly similar, with no hint of the greater utilization of terrestrial habitats by the egrets, as demonstrated by the abundance of terrestrial beetles reported in their food intake.

This study aimed to explore the extent of insects in the diet of Grey Herons and Little Egrets in England, by analysing regurgitated pellets collected from beneath trees in a mixed breeding colony.

Methods

Seventy Grey Heron pellets were collected on 24 October, 17 November, and 4 December in 2020, and 23 April and 23 June in 2021, along with 48 Little Egret pellets that were collected on 28 July 2021, all from the RSPB Northward Hill reserve in Kent, in southeast England. Northward Hill is a 278 ha nature reserve and Site of Special Scientific Interest that overlooks the Thames Marshes. The reserve comprises a working farm, orchards, shrubland, and mixed deciduous woodland. Large populations of Grey Herons and Little Egrets breed in the woodland at Northward Hill (Will Tofts, pers. comm.). Most of the woodland is off-limits to the public, only being disturbed during wildlife surveys or necessary maintenance work. The site has a good population of small mammals, possibly because the site is mainly undisturbed and predatory Red Foxes *Vulpes vulpes* are culled to protect ground-nesting birds (Will Tofts, pers. comm.).

The site was visited five times during this study, which included three supervised visits: two accompanying volunteers conducting Grey Heron breeding surveys, and one just after the Little Egrets had finished breeding. Samples of pellets were collected from under the large trees where the herons were nesting, and below the hawthorn (*Crataegus* spp.) bushes in which the egrets were nesting. The dates were arranged in conjunction with the site warden, with the July date for egret samples arranged so that the nestlings were close to fledging and did not leap from the nests as a result of disturbance. This method of collecting evidence for dietary analysis was deemed the least invasive, particularly when compared to previous work (Dimentiev & Gladkov 1951, Valverde, 1956), where birds were shot and their stomach contents analysed.

Data analysis

All pellets found were photographed *in situ* and then placed individually in numbered bags together with a note of the date, time, location, and the condition of the pellet.

All samples were transported to the laboratory where the mass was recorded, using an Ohaus Adventurer AX5202 balance. The species that produced the sample was assumed to be the bird under whose nest the pellet was collected, and this was checked by reference to identification guides (Bang & Dahlstrom 1974). The samples were then stored by freezing in a Beko F60290N (–20°C) freezer until they could be dissected and further analysed.

The samples were completely defrosted before being teased apart using forceps and separated into their different components, such as bones, hair, exoskeleton, and seeds. The separated samples were then photographed, and the different components were recorded. These components were used to identify the prey (where possible), which was recorded, and some of the items were photographed

Table 1. The various insect species found in Grey Heron pellets.

Species	Habitat	Number of pellets where present	Total number of individuals found	Maximum number of individuals in one pellet
Dytiscidae				
Agabus bipustulatus	Aquatic	1	1	1
Colymbetes fuscus	Aquatic	6	7	2
Dytiscus circumflexus	Aquatic	7	9	2
Dytiscus marginalis	Aquatic	2	2	1
Dytiscus spp. larva	Aquatic	2	2	1
Rhantus frontalis	Aquatic	2	2	1
Hydrophilidae				
Hydrobius fuscipes	Aquatic	2	2	1
Hydrophilus piceus	Aquatic	5	7	2
Chrysomelidae				
Phaedon cochleariae	Terrestrial	1	1	1
Heteroptera				
Ilyocoris cimicoides	Aquatic	3	3	1
Notonecta viridis	Aquatic	1	1	1
Notonecta spp.	Aquatic	2	2	1

under a microscope (Leica EZ4, 8-25× magnification with iPhone XR for bones; Leica M125, 1.25-4× magnification with Canon EOS 550D in the Sackler Bioimaging Laboratory at the London Natural History Museum for insect remains).

When more than one prey species was identified in a sample, all species were recorded but the main prey item was noted. The main prey item was determined based on the quantity and type of remains that were found in the sample, by volume from visual assessment. Thus, if a pellet contained mammal fur and numerous bones, but also one beetle, the main prey item was recorded as the mammal. However, if a pellet contained some mammal fur but multiple beetles, it was decided that the beetles were the main prey, and the mammal fur was present because of a previous meal.

Extraction of insect remains was made especially difficult because the digested matrix in which they were embedded was very sticky. Large or colourful remains were fairly easy to detect, but small dull ones were not, and so these were almost certainly under-represented in the recorded totals. Insect remains were mounted by gluing them with gum tragacanth on strips of card, with one strip per pellet, and then allowed to dry before photography.

Identification of the insect remains was achieved by comparing the recovered fragments with named modern material in the collection of the Natural History Museum.

Habitat and size data for the prey insects were taken from Duff (2022; Carabidae, Histeridae, Silphidae), Lindroth (1974; Carabidae), Halstead (1963; Lane et al. 2020; Histeridae), Foster & Friday (2011; Dytiscidae, Gyrinidae), Foster *et al.* (2014; Hydrophilidae), Lott & Anderson (2011; Staphylinidae), Jessop (1986; Scarabaeidae), Joy (1932; Byrrhidae, Elateridae, Chrysomelidae), and Majerus (1994; Coccinellidae). The *Dytiscus* larval length is from Guignot (1947) and the *Hydrophilus* larval length is from Hammond *et al.* (2019).

To determine whether there was a difference in the size of insects consumed by the two heron species at Northward Hill, we compared the median point of the length ranges of their prey species. A Shapiro–Wilk test showed that the prey size data were not normally distributed for either the Little Egrets ($W = 0.683$, $P < 0.001$) or Grey Herons ($W = 0.906$, $P < 0.01$). Therefore, a non-parametric Mann–Whitney U test was used to compare data for the two species. These statistical analyses were performed using RStudio (version 1.4.1106; RStudio Team 2021) using the programming language 'R' (version 4.0.5; R core team, 2021).

Results

The nomenclature for beetles follows Duff (2012) and for water bugs Macan (1965). Of the 70 Grey Heron pellets analysed, only 24 contained insect remains. In total, 12 insect species from four families were identified (Table 1), with approximately 92% of the species consumed by Grey Herons being aquatic. The maximum number of insect species found in a single pellet was four, while the mean was two. A similar number was found for individual insects per pellet, with the maximum being four and the mean being two. The diving beetle *Dytiscus circumflexus* was the species found in the greatest number of pellets, and this also comprised the most prevalent number of individuals.

In contrast, the majority of Little Egret pellets that were analysed (43 out of 48) contained insect remains. The majority of the species consumed by Little Egrets were terrestrial insects (71%), which were identified as 32 species from 10 families (Table 2). On average,

Table 2. The terrestrial insect species found in 48 Little Egret pellets.

Species	Number of pellets where present	Total number of individuals found	Maximum number of individuals in one pellet
Carabidae			
Brachinus crepitans	1	2	2
Carabus violaceus	1	1	1
Blethisa multipunctata	2	2	1
Elaphrus cupreus	1	1	1
Poecilus cupreus	22	26	2
Pterostichus madidus	2	2	1
Pterostichus nigrita/rhaeticus	3	3	1
Pterostichus melanarius	3	3	1
Pterostichus vernalis	2	1	1
Agonum marginatum	1	1	1
Amara similata	3	3	1
Amara spp.	5	5	1
Harpalus rufipes	3	3	1
Harpalus affinis	4	5	2
Harpalus rubripes	1	1	1
Scybalicus oblongiusculus	1	1	1
Chlaenius nigricornis	5	5	1
Hydrophilidae			
Sphaeridium scarabaeoides	1	1	1
Coelostoma orbiculare	2	2	1
Histeridae			
Hister quadrimaculatus	1	2	2
Margarinotus ventralis	1	1	1
Silphidae			
Silpha tristis	2	2	1
Staphylinidae			
Philonthus punctus	1	1	1
Ocypus olens	4	4	1
Ocypus spp. larval mandibles	4	6	3
Tasgius winkleri	1	1	1
Scarabaeidae			
Aphodius ater	2	2	1
Onthophagus medius	3	3	1
Byrrhidae			
Byrrhus pilula	4	5	2
Elateridae			
Agriotes acuminatus	3	3	1
Agriotes lineatus	8	9	2
Agriotes obscurus	1	1	1
Coccinellidae			
Coccinella septempunctata	2	2	1
Chrysomelidae			
Prasocuris phelandrii	1	1	1

each pellet contained three individuals and three species, with the maximum number of species and individuals found in a single pellet being six and nine, respectively. Most of the species identified came from the ground beetle family Carabidae, with one species, *Poecilus cupreus* – with 26 individuals identified across 22 pellets, the most prevalent species by far.

In addition, 12 species from four families of aquatic insects were identified in the pellets of the Little Egrets (Table 3). The number of species found in each pellet ranged from one to three, with the mean number of species per pellet being two. The average number of individuals found in a single pellet was three, but the maximum found in a single pellet was 13. The most numerous individuals found in the Little Egret pellets were *Hydrobius fuscipes*, but both *H. fuscipes* and *Colymbetes fuscus* were present in the greatest number of pellets.

The size of the insect species consumed by the Grey Herons and Little Egrets at Northward Hill were found to be significantly different (*Mann–Whitney* U *test*, $W = 745.5$, $P < 0.001$). Figure 1 suggests that, even though the Grey Heron data are few, they consumed an even spread of larger species with lengths ranging from 10 to 60 mm. The single small item was an isolated elytron of the terrestrial metallic blue chrysomelid beetle *Phaedon cochleariae*. The occurrence of this single, very conspicuous elytron suggests that it may have come from the stomach contents of a mammalian prey item, a conclusion supported by the mammal hairs that were a conspicuous component of the pellet in which the elytron was found.

Little Egrets appeared to have a preference for prey items with a length range of 5–15 mm, almost all from a total length range of 0–17 mm (Figure 1). The exceptional large prey item (to 60 mm) was based on

Table 3. The aquatic insect species found in 48 Little Egret pellets.

Species	Number of pellets where present	Total number of individuals found	Maximum number of individuals in one pellet
Gyrinidae			
Gyrinus substriatus	1	1	1
Dytiscidae			
Agabus bipustulatus	1	1	1
Agabus conspersus	1	1	1
Ilybius fenestratus	2	2	1
Colymbetes fuscus	8	8	1
Rhantus frontalis	4	4	1
Hydaticus seminiger	1	1	1
Hydrophilidae			
Paracymus aeneus	1	1	1
Hydrobius fuscipes	8	15	4
Limnoxenus niger	5	13	8
Hydrophilus piceus	1	1	1
Heteroptera			
Ilyocoris cimicoides	3	3	1

a single head of a *Hydrophilus piceus* larva, a soft-bodied slow-moving animal, and it is interesting to note that no adults of this species, nor those of *Dytiscus* species, were found in the egret pellets.

Discussion

In this study, we have outlined the striking differences between the diets of the two heron species. Grey Heron pellets contained relatively few insects, which were mostly aquatic in origin, whereas Little Egret pellets contained many insects of both aquatic and terrestrial origin.

Habitats of prey species

For Grey Heron pellets, all of the aquatic species they contained were characteristic of standing open water. The diving beetle, *Dytiscus circumflexus*, was the most numerous insect prey item in terms of both individuals and pellets, and is a mainly brackish water species, while *Limnoxenus niger* inhabits brackish as well as freshwater. Brackish water habitats are abundant in the Thames marshes that neighbour the study site. It may be noted that *Dytiscus* diving beetles were recorded as the most abundant invertebrate prey items of Grey Herons in Poland (Jakubas & Mioduszewska 2005) and that *D. marginalis* was recorded as a significant component of the summer diet of Grey Herons in West Stirlingshire, Scotland (Giles, 1981). The terrestrial *Phaedon cochleariae* feeds on crucifers (Brassicaceae) and is mentioned as a pest of mustard plants by Joy (1932).

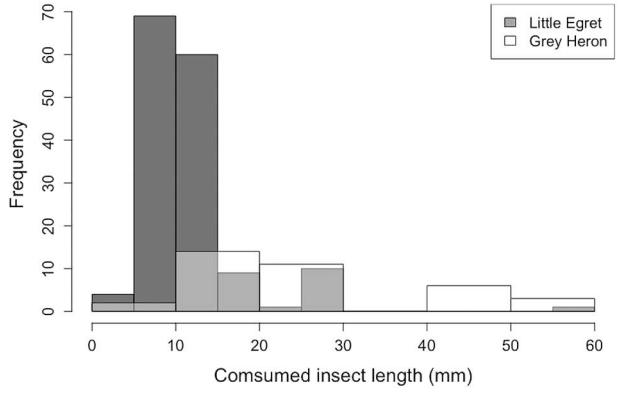

Figure 1. Histogram showing the varying sizes of prey items found Grey Heron and Little Egret pellets.

For Little Egrets, 16 of the 32 terrestrial species identified in pellets were carnivorous ground beetles (Carabidae), mostly associated with damp (sometimes waterside) or mesic habitats. A few, however, are associated with dry, arid habitats. These include the Bombardier Beetle *Brachinus crepitans*, mainly associated with chalk and limestone, and *Scybalicus oblongiusculus*, originally found (in Britain) on Portland Bill in 1878 and regarded by Lindroth (1974) as 'undoubtedly introduced', although considered a probable native by Telfer (2016). This species is associated with dry habitats, including brownfield sites. Species of the other families present in the sample are generally associated with damp or mesic habitats, mainly of open ground. The staphylinid *Philonthus punctus* is associated with ground subject to flooding and is characteristic of the Thames estuary saltmarshes.

The diversity of terrestrial species per pellet was generally low, with a maximum of six per pellet (in one pellet), and most pellets contained between one and three species. Most pellets had from one to five individual beetles, with one pellet having seven and another nine. Most species were represented by singletons in individual pellets, with some occurring as twos, and one (*Ocypus olens*, larval mandibles) as three in a pellet. The pellet with the most species

associated with dry habitats, *B. crepitans* and *S. oblongiusculus*, did not contain any aquatic or damp-associated terrestrial species.

The insect diet of Little Egrets is discussed by Valverde (1956) and Dementiev & Gladkov (1951). As mentioned in the Introduction, all of the Coleoptera and Heteroptera named by Valverde are aquatic, but terrestrial Orthoptera, namely mole-crickets *Gryllotalpa* spp. and crickets *Gryllus* spp. are also included (Dementiev & Gladkov 1951, Cramp *et al.* 1977). In their discussion of Russian data, these sources list mainly aquatic insects, but note that in the second half of summer Orthoptera become important, with large numbers of grasshoppers, locusts, and crickets being found in egrets' stomachs. Valverde stated that the Little Egret is a daytime and crepuscular (dusk) feeder, and crepuscular feeding could account for the presence of mole-crickets in the diet, as these subterranean insects emerge and fly in the evening and at night.

Most of the aquatic species found in pellets were typical of still freshwater in exposed places; *Agabus conspersus* is associated with brackish water, and the habitat of *Limnoxenus niger* also includes brackish water, while *Hydaticus seminiger* tends to favour shaded places. As with the terrestrial species, most pellets contained only one or two species, though three pellets contained three species and one had four *Hydrobius fuscipes* individuals and eight *Limnoxenus niger*. Another pellet had three *H. fuscipes* and two *L. niger*. These numbers are likely to result from the habit of Little Egrets of stirring the water with their feet, as originally noted by Moule (1953). Both *H. fuscipes* and *L. niger* are fairly feeble swimmers, and are brought to the water surface by this type of stirring. This may explain the occasional clusters of these species, while the terrestrial species were generally caught one at a time.

Apparent failure of distastefulness to protect prey species

Several of the prey species of both Little Egrets and Grey Herons are characterized by pungent secretions that are very unpleasant to humans. This is the case with various carabid ground beetles, staphylinid rove beetles, and some dytiscid diving beetles. Thus, Foster & Friday (2011) noted the presence of *Ilybius fenestratus* in large angling lakes, possibly protected by its pungent smell. Some important differences between avian and mammalian taste receptors are well-known, a prime example being the ineffectiveness of the capsaicin present in chilli peppers in deterring birds, which is correlated with their role in dispersing seeds (see Tewkbury & Nabhan 2001). More surprising is the predation of the Bombardier Beetle *Brachinus crepitans* by one Little Egret in the current study, whose pellet contained elytra of two individual Bombardiers. These beetles create explosive emissions from their rear ends by mixing various chemicals, including hydrogen peroxide, in their recta (Crowson 1981, Osterloff 2019).

Conclusions

The data reported here show that the examination of pellets provides a straightforward, easily replicable, and non-invasive insight into the diet of pellet-producing birds. Similar work should be repeated at different times of the year, at more localities, and for more species of the family Ardeidae, such as the recently arrived Cattle Egret *Bubulcus ibis* in Britain, thought to be one of the most insectivorous members of the heron family. Future research could also compare results from hand-picking and visual identification of insect fragments with those obtained from DNA-barcoding methods.

Acknowledgements

We thank Will Tofts and Joseph Tilbury of the RSPB, as without access to Northward Hill and their knowledge of the reserve this data collection could not have taken place. We further thank the Natural History Museum, in London, for the use of its collections and laboratory facilities, including photographic, and Dr Boris Korotyaev for providing a pdf of the relevant part of Dementiev & Gladkov's work, and for helping with the translation from Russian.

Disclosure statement

No potential conflict of interest was reported by the author(s).

ORCID

Maxwell V. L. Barclay http://orcid.org/0000-0003-4989-2014

References

Bang, P. & Dahlstrom, P. 1974. *Collins Guide to Animal Tracks and Signs*. Collins Sons & Co. Ltd, Glasgow.

Cramp, S., Simmons, K.E.L., Ferguson-Lees, I.J., Nicholson, E.M., Ogilvie, M.A., Olney, P.J.S., Voous, K.H. & Wattel, J. (eds) 1977. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palearctic 1: Ostrich to Ducks*. Vol. 1: 292–293, 306–307. Oxford University Press, London.

Crowson, R.A. 1981. *The Biology of the Coleoptera. Vol. 802*. Academic Press, London.

Dementiev, G.P. & Gladkov, N.A. 1951. *Birds of the USSR*. Vol. 2. Academy of Sciences of the USSR, Moscow-Leningrad. (In Russian).

Duff, A.G. (ed) 2012. *Checklist of Beetles of the British Isles, revised edition*. Vol. 171. Pemberley Books, Iver.

Duff, A.G. 2022. *Beetles of Britain and Ireland. Volume 1: Sphaeriusidae to Silphidae*. A. G. Duff Publishing, Norfolk.

Foster, G.N., Bilton, D.T. & Friday, L.E. 2014. *Keys to the adults of the water beetles of Britain and Ireland (Part 2) (Coleoptera: Polyphaga: Hydrophiloidea – both aquatic and terrestrial species) R. Entomol. Soc. Handb. Identif. British Insects* **4** (5b): 126. Field Studies Council, Shrewsbury.

Foster, G.N. & Friday, L.E. 2011. *Keys to the adults of the water beetles of Britain and Ireland (Part 1). R. Entomol. Soc. Handb. Identif. British Insects* **4** (5): 144. Field Studies Council, Shrewsbury.

Giles, N. 1981. Summer diet of the Grey Heron. *Scott. Birds* **11:** 153–159.

Guignot, F. 1947. *Faune de France 48. Coléoptères Hydrocanthares*. Vol. 287. Lechevalier, Paris.

Halstead, D.G.H. 1963. *Coleoptera. Histeroidea. Royal Entomological Society Handbooks for the Identification of British Insects*. Vol. 4 (10):16. Royal Entomological Society, London.

Hammond, P.M., Marshall, J.E., Cox, M.L., Jessop, L., Garner, B.H. & Barclay, M.V.L. 2019. British Coleoptera larvae. A guide to the families and major subfamilies. *R. Entomol. Soc. Handb. Identif. British Insects* **4** (1a): 280. Field Studies Council, Shrewsbury.

Jakubas, D. & Mioduszewska, A. 2005. Diet composition and food consumption of the Grey Heron (*Ardea cinerea*) from breeding colonies in northern Poland. *Eur. J. Wildl. Res.* **51:** 191–198.

Jessop, L. 1986. Dung Beetles and Chafers, Coleoptera: Scarabaeoidea. *R. Entomol. Soc. Handb. Identif. British Insects.* **5** (11):53. Royal Entomological Society, London.

Joy, N.H. 1932. *A Practical Handbook of British Beetles*. Vol. 1. E.W. Classey Ltd., London.

Lane, S.A., Lucas, C.B.H. & Whiffin, A.L. 2020. *The Histeridae, Sphaeritidae and Silphidae of Britain and Ireland*: 360. Field Studies Council, Telford.

Lindroth, C.H. 1974. Coleoptera. Carabidae. *R. Entomol. Soc. Handb. Identif. British Insects.* **4** (2):148. Royal Entomological Society, London.

Lott, D.A. & Anderson, R. 2011. *The Staphylinidae (rove beetles) of Britain and Ireland Parts 7 & 8: Oxyporinae, Steninae, Euaesthetinae, Pseudopsinae*, Paederinae Staphylininae. *R. Entomol. Soc. Handb. Identif. British Insects.* **12** (7): 340. Field Studies Council, Shrewsbury.

Macan, T.T. 1965. *A Revised key to the British Water Bugs (Hemiptera – Heteroptera) with Notes on Their Ecology*. 2nd edn. Freshwater Biological Association, Ambleside.

Majerus, M.E.N. 1994. *Ladybirds. New Naturalist*. Harper Collins, London.

Marquiss, M. & Leitch, A.F. 1990. The diet of the Grey Heron *Ardea cinerea* breeding at Loch Leven, Scotland, and the importance of their predation on ducklings. *Ibis* **132:** 535–549.

Moltoni, E. 1936. Le Garzaie in Italia. *Riv. Ital. Orn.* **6:** 109–148.

Moule, G.W.H. 1953. Feeding habits of the Little Egret. *Br. Birds* **46:** 258.

Osterloff, E. 2019. Bombardier beetles and their caustic chemical cannon. Available at: https://www.nhm.ac.uk/discover/bombardier-beetles-and-their-caustic-chemical-cannon.html (accessed 19/12/2022).

R Core Team. 2021. R: A Language and Environment of Statistical Computing. R foundation for statistical computing, Vienna, Austria. URL: https://www.R-project.org/

RStudio Team. 2021. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. URL: https://www.rstudio.com.

Telfer, M.G. 2016. A review of the Beetles of Great Britain: ground beetles (Carabidae): Species Status No. 25. *NECRS* **189**.

Tewkbury, J.J. & Nabhan, G.P. 2001. Directed deterrence by capsaicin in chillis. *Nature* **412:** 403–404.

Valverde, J.A. 1956. Essai sur l'Aigrette garzette (*Egretta garzetta*) en France. *Alauda* **24:** 1–36. (in French).

Wood, K.A. & Stillman, R.A. 2014. Do birds of a feather flock together? Comparing habitat preferences of piscivorous birds in a lowland river catchment. *Hydrobiologia* **738:** 87–95.