A complete dietary review of Japanese birds with special focus on molluscs

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Birds often hold important positions in the food webs of ecosystems. As a result, interactions between birds and their prey have attracted attention not only in ecology, but also in fields like agriculture and conservation. Avian food resources are well researched in Japan, however there is no database critically reviewing molluscs as a food resource for birds. Here, we present a new database reviewing dietary information for all Japanese bird species. In addition to addressing general diet categories and specific food habits for each bird, we include detailed data on the molluscan prey observed for all species that consume them. The information within this database was collected through intense literary review to provide a complete look at bird species historically present around the country. We also include new information on snail species found in the upper digestive tract of harvested wild birds. This database is publicly available in the Zenodo repository. The information should aid research around the Japanese archipelago, especially projects involving birds or molluscs.

Background & Summary
Ornithology has long been one of the main fields of naturalist study and significant knowledge has been accumulated during its long history1-2. Birds have some advantages for scientific research: (1) compared to other taxa, birds are easier to detect and identify via vocalization and are often less cryptic with fewer overall species than other macroorganisms1; (2) the occurrence, abundance, and reproductive success of birds has been shown to respond to environmental changes over many spatial scales3; (3) birds are often very popular flagship species for conservation and important for government policies4,5; and (4) the large volume of accumulated ornithological knowledge allows for strong review and cross-referencing of new research6,7.

Birds assume many fundamental ecological functions in the maintenance of local to continental-scale ecosystems. Their roles include dispersion of seeds, pollination, and long distance transfer and/or deposition of nutrients8-12. At the same time, birds are often in important positions as keystone and/or umbrella species in various community food webs13-17. In particular, the predator-prey interactions between birds and insects are well known: more than 50% of avian species are predominantly insectivorous, and nearly 75% prey on invertebrates at least occasionally16,18. Birds can reduce the densities of herbivorous insects in agriculture and may exert top-down effects on primary producers to the extent that their removal instigates trophic cascades19,20. Various investigations have shown that birds contribute significantly to agricultural success especially where they prey upon insects that are detrimental to human activities17,20. Thus, it is important to understand basic information about the food preferences of each bird species not only for ecological science but also for practical applications.

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diet consists almost entirely of freshwater snails in the Americas. Even for land snails, omnivorous birds are considered as regular predators. Another example, the Great Tit (Parus major; Paridae, Passeriformes) and some other forest passerines in Eurasia take land snails as the main component of their diet. Among regions there tends to be strong observation and research biases dependent on population, economy, and resource availability. These area-based biases can skew understandings of real diversity on earth and prevent comprehensive insights from being made. In this study, we investigated the diet of all bird species in Japan, with a special focus on molluscan prey. The Japanese archipelago and associated islands are located from the subarctic to the subtropical zone, therefore this area has high biodiversity and the region is recognized as a hotspot for the planet. Similarly to other regions, ornithology in Japan has a long history and rich data to work from, but few researchers have reviewed the food preferences of all local bird species. Moreover, many publications reporting on the food composition of Japanese birds were written in Japanese, so it is difficult to disseminate this knowledge widely given the language barrier. There are some excellent works and databases showcasing the ecological traits of the entire avian fauna of Japan, but they are only available in Japanese.

Most databases fail to identify molluscan prey at the species level despite wide variability within the phylum. It is important to determine the exact interactions between predator and prey at the species level due to ecological differences and unique conservation considerations for each party to a predatory interaction. In this study, we attempted to classify the main diet of all Japanese bird species, list detailed information on molluscs in avian diets, and evaluate molluscs as a food resource for birds based on available literature. We also newly record five species of molluscs as avian food resources (I-iv: freshwater molluscs, iv-f: marine gastropods, iv-mb: marine bivalves, iv-mc: marine cephalopods, or iv-o: others or unknown molluscs). We also newly record five species of molluscs as avian food resources (I: some of animals, II: some of plants, I-i: fishes, I-ii: vertebrates, I-iii: arthropods, I-iv: molluscs, I-v: unknown or other animals, II-fr: plants (fruits and/or seeds), II-le: plants (leaves and/or others), or III: scavenger).

### Table 1. Description of each variable, and factor levels.

| 1. the distribution and breeding status | The bird distribution and residency in each area of Japan. RB: resident breeder, MB: migrant breeder, WV: winter visitor, PV: passage visitor, FB: former breeder, or —: not distributed, rare or unknown (see also Fig. 1). |
| 2. the endemicity in Japan | Endemic, or —: not endemic to Japan. |
| 3. the species status in the Japanese Red List | The seven categories of species status based on the 2020, 4th Version of the Japanese Red Lists. EX: extinct, CR: critically endangered, EN: endangered, VU: vulnerable, NT: near threatened, DD: data deficient, or —: common species or not listed. |
| 4. main habitat | Main habitat. Terrestrial, Freshwater, and/or Marine, or Unknown. |
| 5. dietary categories | I: carnivore, II: herbivore, IV: omnivore, or Unknown (see also Fig. 2). |
| 6. main diet(s) | Main diet(s): I: some of animals, II: some of plants, I-i: fishes, I-ii: vertebrates, I-iii: arthropods, I-iv: molluscs, I-v: unknown or other animals, II-fr: plants (fruits and/or seeds), II-le: plants (leaves and/or others), or III: scavenger (see also Fig. 2). |
| 7. all recorded food habits | All recorded food habits of each bird species. I: some of animals, II: some of plants, I-i: fishes, I-ii: vertebrates, I-iii: arthropods, I-iv: molluscs, I-v: unknown or other animals, II-fr: plants (fruits and/or seeds), II-le: plants (leaves and/or others), or III: scavenger (see also Fig. 2). |
| 8. molluscs as avian food resources | Six categories of molluscs as avian food resources (I-iv: freshwater molluscs, iv-f: marine gastropods, iv-mb: marine bivalves, iv-mc: marine cephalopods, or iv-o: others or unknown molluscs). |
| 9. descriptions of molluscan prey in literature | The descriptions of molluscan prey and their taxonomies in literature. |
| 10. referenced bibliographies | Referenced papers and books (shown in the reference list on Zenodo). |

It is well established that birds prey on molluscs in various environments. Many species of sea ducks (Anatidae, tribe mergini) prey on bivalves and have economic impacts on mussel farms worldwide. The Snail Kite (Rostrhamus sociabilis; Accipitridae, Accipitriformes) and Limpkin’s (Aramus guarauna; Aramidae, Gruiformes) diet consists almost entirely of freshwater snails in the Americas. Even for land snails, omnivorous birds are considered as regular predators (e.g., Turdus spp.; Muscicapidae, Passeriformes). Another example, the Great Tit (Parus major; Paridae, Passeriformes) and some other forest passerines in Eurasia take land snails as the main calcium source for eggshell production. Despite these well documented instances, the scope of interactions between birds and molluscs is much less surveyed than between birds and insects.

Avian ecological databases have been established in several regions (e.g., Europe, North America, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International, Avibase, BirdLife International, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International). Avian ecological databases have been established in several regions (e.g., Europe, North America, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International, Avibase, BirdLife International, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International). Avian ecological databases have been established in several regions (e.g., Europe, North America, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International, Avibase, BirdLife International, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International, Avibase, BirdLife International, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International, Avibase, BirdLife International, Australia, New Zealand, the North Pacific, and Antarctica) while others have global scope (e.g., BirdLife International, Avibase, BirdLife International, Australia, New Zealand, the North Pacific, and Antarctica). Several platforms for citizen science also contribute to avian knowledge (e.g., eBird, iNaturalist, and GBIF). However, most of these databases mainly focus attention on avian distributions, and often do not provide great detail on dietary preferences or predator-prey interactions. Moreover, very few databases recorded prey species in these categories instead providing general overviews of diet.

Methods Classification of dietary preferences and habitats for bird species in Japan via literature. We reviewed the food habits of 633 native avian species listed in the Check-list of Japanese Birds, 7th Revised Edition in attempting to represent the whole avian fauna of Japan. Nine ecological traits related to distribution, habitat and diet are listed in our database along with references as shown below (Table 1): (1) the distribution and breeding status in each region of Japan (Fig. 1), (2) the endemicity in Japan (Endemic, or —: not endemic to Japan), (3) the species status in the Red List of Threatened Species of Japan, (4) main habitat (Terrestrial, Freshwater, and/or Marine, or Unknown), (5) dietary categories (I: carnivore, II: herbivore, IV: omnivore, or Unknown; Fig. 2), (6) main diet(s) (I: some animals, II: some plants, I-i: fishes, I-ii: vertebrates, I-iii: arthropods, I-iv: molluscs, I-v: unknown or other animals, II-fr: plants (fruits and/or seeds), II-le: plants (leaves and/or others), or III: scavenger).
unknown or other animals, II-fr: plants [fruits and/or seeds], and/or III: scavenger, or Unknown; Fig. 2), (7) all recorded food habits (I-i, I-ii, I-iii, I-iv, I-v, II-fr, II-le: plants [leaves and/or others], or III; Fig. 2), (8) molluscs as avian food resources (iv-t: terrestrial molluscs, iv-f: freshwater molluscs, iv-mg: marine gastropods, iv-mb: marine bivalves, iv-mc: marine cephalopods, or iv-o: others or unknown molluscs; Fig. 2), (9) descriptions of molluscan prey in literature, and (10) referenced bibliographies.

To keep our findings relevant, we reviewed the validity of species binomial names listed in our database and provide updates reflective of current taxonomic knowledge in 2020. A review was conducted using the Birds of the World online research database and apparent updates to binomials were cross-referenced using the

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**Fig. 1** Seven categories of distribution area in this study.
### Categories of food habit for each bird species

| I. Animals (carnivore) | II. Plants (herbivore) | III. Scavenger | IV. Omnivore |
|------------------------|------------------------|----------------|--------------|
| Fruits and/or seeds (I-f) |
| Leaves and/or others (I-le) |
| I-i. Fishes in freshwater (i-f) or sea (i-m) |
| I-ii. Vertebrates without fishes on land (i-i-t) or in freshwater (amphibians; ii-f) |
| I-iii. Arthropods on land (iii-i), in freshwater (iii-f) or sea (iii-m) |
| I-iv. Other or unknown animals on land (v-i), in freshwater (v-f) or sea (v-m) |
| I-iv. Molluscs |
| Terrestrial molluscs (land snails; iv-t) |
| Freshwater molluscs (iv-f) |
| Marine gastropods (iv-mg) |
| Marine bivalves (iv-mb) |
| Marine cephalopods (iv-mc) |
| Other or unknown molluscs (iv-o) |

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**Fig. 2** The categories of preferred foods in this study. Food preferences were first categorized into four big groups (I: carnivore, II: herbivore, III: scavenger and IV: omnivore), and two of them (I and II) were further separated. In particular, molluscs were classified in detail.

International Union for Conservation of Nature’s Red List of Threatened Species (https://www.iucnredlist.org). The updated binomial information is included in Online-only Table 1.

We roughly categorized seven regions for avian distribution in the Japanese archipelago (Hok: Hokkaido Island and/or surrounding islands, Hon: Honshu Island and/or surrounding islands, Shi: Shikoku Island and/or surrounding islands, Kyu: Kyushu Island and/or surrounding islands, Ryu: Ryukyu archipelago, Izu: Izu islands, Oga: Ogasawara islands; Fig. 1), and classified six categories for residency in each region of Japan (RB: resident breeder, MB: migrant breeder, WV: winter visitor, PV: passage visitor, FB: former breeder, or −: not distributed, rare, or unknown) based on the Check-list of Japanese Birds, 7th Revised Edition39, and added seven categories for the species status in Japan based on the 2020, 4th Version of the Japanese Red Lists (EX: extinct, CR: critically endangered, EN: endangered, VU: vulnerable, NT: near threatened, DD: data deficient, or −: common species or not listed)5. To determine each species' main diet, we primarily focused on literature describing "preferred" or "main" food habits, although we also utilized information about the frequency of target foods in crop and gizzard contents. The taxonomies of molluscan prey written in the database were mainly based on MolluscanBase (http://www.molluscanbase.org), the online database of world mollusc classifications. While our database does not contain perfect information on distribution, residency, and conservation status in terms of current knowledge, we believe it represents a high degree of accuracy and usefulness in pulling together comprehensive information from different sources.

The diet data in this study was collected from 165 scientific articles and books including dietary information on Japanese birds. We searched for the following two series of keywords in Google Scholar for each bird species: [{"scientific name" AND ["food habits" OR "diet" OR "food habits (in Japanese)" OR "crop and gizzard contents (in Japanese)"]} and {"standard Japanese name (in Japanese)" AND ["food habits" OR "diet" OR "food habits (in Japanese)" OR "crop and gizzard contents (in Japanese)" ]}. Keyword searching and browsing was conducted between 2nd May and 27th December in 2017, and the top one-hundred and all results for each series of keywords was checked, respectively. Moreover, we manually reviewed additional several literatures and books as possible. These included publications in English and Japanese and were published between 1913 and 2018. All 165 references citing the food habits for each bird species are recorded in the database, and listed on the reference list in Zenodo40.

**Land snails detected from the crop and gizzard of two bird species in Hokkaido, Japan.** Crop and gizzard samples were obtained from two juvenile Oriental Turtle-Doves (Streptopelia orientalis; Columbidae,
Columbiformes; Fig. 3A) and one juvenile Hazel Grouse (Tetrastes bonasia; Phasianidae, Galliformes; Fig. 3B). An individual T. bonasia was hunted at Ubaranai site no. 1 (Abashiri City, Hokkaido, Japan; N 43.9678°, E 144.0414°) on 7 November 2013, and two S. orientalis were shot at Ubaranai site no. 2 (Abashiri City, Hokkaido, Japan; N 43.9261°, E 144.0406°) on 28 October 2016. These birds were shot by a professional hunter for food and stored in a freezer; we then received them from the hunter and carefully extracted the crop and gizzard contents. Crop and gizzard contents of T. bonasia were identified from a photograph, while those of S. orientalis were identified directly from samples. In addition, the combined weight of crop and gizzard contents were measured for both S. orientalis individuals using an electronic scale (wet and dry weights for one, and dry weight only for the other; Online-only Table 2). The data collected from these samples is also included in our database.

Data Records
The database for the ecological traits of birds in Japan is available on Zenodo with the original database in XLSX format (i.e. “Whole_Database.xlsx” on Zenodo), the reference list correspond to the database in PDF and CSV format (i.e. “Reference_List.pdf” and “Reference_List.csv” on Zenodo), and ten different data files for each trait category with described names provided in CSV format. For CSV format files on Zenodo, we used “0” and “1” instead of “−” and “+” in original database, respectively, “Unknown” for the missing data of mid three traits (i.e. variable no. 4, 5 and 6) like as in original database, and “NULL” for the non-existing values on the last four variables (i.e. variable no. 7, 8, 9 and 10). We also included the literary references as numbers in the data files as shown in “Reference_List.pdf” and “Reference_List.csv” on Zenodo. The first row of each CSV data file shows the description of each file, the second row includes a header indicating the names of variables, and the following rows present data for each bird species in Japan. The crop and gizzard contents from two individuals of S. orientalis used in this study were stored in Bihoro Museum (Bihoro, Hokkaido, Japan; Specimen IDs: BIHM0300372 and BIHM0300373).

Fig. 3 (A,B) Two bird species investigated in this study, Streptopelia orientalis (A), and Tetrastes bonasia (B). (C–H) The prey items detected from avian crops and gizzards of S. orientalis, (C) Cochlicopa lubrica (Cochlicopidae, Stylommatophora), (D) Discus pauper (Discidae, Stylommatophora), (E) Karafothelix (Ezohelix) gainesi (Camaenidae, Stylommatophora), (F) Parakaliella affinis (Helicarionidae, Stylommatophora), (G) Persicaria thunbergii (Polygonacea, Caryophyllales), and (H) Schizopepon bryoniifolius (Cucurbitaceae, Cucurbitales). I. The photograph of crop and gizzard contents of T. bonasia.
Technical Validation
All records included in the database are based on articles in scientific journals and books; therefore we have confidence in their accuracy. We also listed the references cited in the database, making it possible for users to access the original sources. Moreover, some bird specialists, MK and T-Squires and mollusc specialists, Y-Morii, T-Saito and DY have carefully checked the database for possible errors and included information on outdated or updated avian binomials in Online-only Table 1.

Code availability
No code was used in this study.

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Author contributions
Y.-Morii designed the database and wrote the manuscript with T.-Squires. Y.-Morii, M.K., M.W., Y.W., A.U. and Y.-Machida collected the data, and Y.-Morii, M.K., T.-Squires, T.-Saito and D.Y. carefully reviewed and updated the database.

Competing interests
The authors declare no competing interests.

Additional information
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