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Terje Lislevand, Jordi Figuerola, and Tamás Székely. 2007. Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. *Ecology* 88:1605.

INTRODUCTION

The evolution of body size in animals has fascinated biologists for decades. Already Darwin (1871) noted that species vary considerably with respect to the difference in body size among sexes, and the causes and consequences of sexual size dimorphism (SSD) are still much debated issues among evolutionary ecologists (e.g., Andersson and Norberg 1981, Mueller and Meyer 1985, Jehl and Murray 1986, Olsen and Olsen 1987, Mueller 1990, Andersson 1994, Figuerola 1999, Szekely et al. 2000, Dunn et al. 2001, Fairbairn 2005, Shine and Mason 2005, Székely et al. *in press*). Moreover, the inter-specific variation in general body size is itself important and is known to influence a range of other animal characteristics. Hence, body size is recognized as an important correlate in a great number of studies in physiology, ecology and evolutionary biology (LaBarbera 1989), including conservation biology (Purvis et al. 2000), life history (Roff 1992, Stearns 1992, Webster et al. 2004), sexual selection (Andersson 1994), breeding ecology and mating systems (Bennett and Owens 2002), rates of speciation and extinction (Owens et al. 1999) and rates of DNA evolution (Martin and Palumbi 1993).

Comparative methods are powerful tools for studying how aspects of animal ecology, morphology, behavior, and life history have evolved – independently or in concert (Harvey and Pagel 1991, Martins 1996, Blomberg et al. 2003). However, comparative studies are often hampered by low data availability, and the time and effort needed to assemble adequate databases. Here we present a comprehensive data set which makes measurements of avian body sizes and some possible covariates readily accessible. The number of species from which data are included for both sexes ranges between 2350 and 2979 among five different body size measurements. We collected most data from major text books covering the bird faunas of geographical regions where bird ecology and behavior has traditionally been best studied, i.e., the western Palearctic, Africa, Australia, New Zealand, Antarctica, and North America. We have used the data set to study the evolution of SSD in birds, where we tested adaptive hypotheses concerning the influence of fecundity, sexual selection, and within-pair resource sharing. In addition to the body size measurements, we therefore include data on egg size and clutch size, together with scores of mating systems, sexual display agility, and territoriality.

We hope that this data set will facilitate future comparative studies in avian biology. In addition, it points out species where baseline data on body size and/or relevant information on reproduction and behaviour are currently lacking or of poor quality, and thus may stimulate the publication of such data.

METADATA

CLASS I. DATA SET DESCRIPTORS

A. Data set identity: Title: Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing.

B. Data set identification code: avian_ssd_jan07.txt

C. Data set description

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Abstract: Body size is an important characteristic of animals, influencing physiology, life histories, and general ecology. Hence, it often needs to be taken into account even if the aim is to test for relationships among other traits. The aim of this paper is to provide a comprehensive data set on avian body sizes that would be useful for future comparative studies of avian biology. We extracted species-specific measurements on male and female body mass, wing length, tarsus length, bill length, and tail length from major ornithological text books and some other sources covering bird species of Africa, Australia, New Zealand, Antarctica, North America, and the western Palearctic. These measurements were matched with measures of egg and clutch sizes, and scores of mating system, sexual display agility, and the degree of intersexual resource division. We present morphometric data ranging from 2350 species (minimum, tail length) to 2979 species (maximum, wing length) where measurements for both sexes are known, some additional data where only one sex or unsexed birds have been measured, and explanatory data ranging from 1218 species (minimum, display agility) to 2603 species (maximum, egg mass). In total, 3769 species from 125 of 146 different bird families are included. We have used the data in comparative studies of avian sexual size dimorphism, where we test adaptive hypotheses concerning the influence of sexual selection, fecundity, and

the degree of within-pair resource sharing. By publishing the data we intend to give easy access to a large data set containing variables relevant for a wide range of comparative studies on birds, thus saving researchers from the time- and resource-consuming data gathering process. In addition, the data set will function to point out species where baseline data on body size and relevant information on reproduction and behavior are currently lacking or of poor quality, thus stimulating the publication of such data.

D. *Key words*: *allometry; birds;, body size; clutch size; egg size; mating systems; niche separation; sexual display; sexual selection; sexual size dimorphism.*

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description

Identity: Evolution of sexual size dimorphism in birds

Originator: Tamás Székely
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Period of Study: 2005-continuing

Objectives: To enhance the understanding of body size evolution in birds, in particular the evolution of sexual body size dimorphism.

Abstract: Same as above.

Sources of funding:T. Székely was funded by a Leverhulme Research Fellowship (RF/2/RFG/2005/0279), by the BBSRC (BBS/B/05788) and NERC (NE/C004167/1). J. Figuerola was funded by the Ramón y Cajal Program of Ministerio de Educación y Ciencia.

B. Specific subproject description

Site description: Data collection was focused on the geographic regions of Western Palearctic, Nearctic, Africa, Australia, New Zealand, and Antarctica. Species are included in the data set regardless of their habitat preferences.

Experimental design: Data were collected from the literature or by personal communication with other researchers.

Research methods:

Field/Laboratory: n/a

Data sources:For the majority of species, data were extracted from major ornithological handbooks (Handbook of birds of the Western Palearctic, Birds of North America online, Birds of Africa and Handbook of the Birds of Australia, New Zealand, and Antarctica). Some data were also obtained from some data sets used in previous publications on specific bird groups and by personal communication with specialists on the species in question. All references for data sources are given in Class V Supplemental Descriptors, Section F.

Data Collection: We collated data from the literature on male and female body mass, wing length (flattened wing), tarsus length, bill length (tip to feathers) and tail length. We started out with the data set of Dunn et al. (2001) including more than 1000 species, but for consistency we replaced these entries with data from our own sources in cases of overlap. As far as possible, morphometric data were taken from adult birds, and body mass data from the breeding season. If several data points were available for a given variable and species, we chose those based on the largest sample sizes. However, if data on several variables were reported from specific locations, we did not split these data series but chose the one with highest sample size for body mass.

Our original intention with producing the data set was to carry out comparative studies of sexual size dimorphism in birds. Hence, for consistency, we avoided extracting data from sources reporting species as sexually size monomorphic if differences between sexes were smaller than some arbitrary limit. Note, however, that a number of such data points were taken from Dunning (1993) either (1) because they were entered by us at an early stage and mistakenly not excluded, or (2) they existed in data sets acquired from other researchers who used them in published studies. Since these data were included in the analyses of our first publication building on the data set (Székely et al., *in press*), we also include them here identified by the reference number 51.

In most cases and for all variables we have used mean values, either as described by the source or as calculated from raw data. We have generally followed a rule of not incorporating data calculated as midpoints of ranges as there is the possibility that these are somewhat skewed compared to mean values. However, in some studies of restricted bird groups, many authors (including ourselves) have used midpoints of body size ranges to increase sample sizes. When incorporating such data sets in the present data paper, we have not deleted the values calculated from ranges. Data on body mass, clutch and egg size from birds in captivity were not included. With regard to the behavior variables, we collated written descriptions of the behavior in question for each species, and subsequently scored these according to predefined definitions (see categories below).

Behavioral scores:

<u>Mating competition/mating system:</u> Categories were taken from Dunn et al. (2001), or from textbook descriptions using the following categories: (1) polyandry; (2) monogamy (<5% polygyny); (3) mostly monogamy, but occasional polygyny (5–15% polygyny); (4) mostly polygyny (> 15% polygyny) and (5) lek or promiscuous. This scoring reflects the notion that the intensity of male-male competition increases from 1 to 5. Note that cooperative breeders (score 5 in Dunn et al. 2001, n = 103 species) were merged with monogamous species (n = 954 species).

<u>Sexual display behavior:</u> We produced the scores independently of each other, and blindly with regard to species name and other information in the data set. Median scores are given for each species. We scored literature descriptions of male display behaviours on a five point scale as follows: (1)

ground displays only, including displays on trees and bushes; (2) ground displays, but with occasional jumps/leaps into the air; (3) both ground and non-acrobatic flight displays; (4) mainly aerial displays, non-acrobatic; (5) mainly aerial displays, acrobatic. A display was considered acrobatic if it included rapid changes in flight direction, twists, rolls and turns. The scores were highly consistent among observers (r_S = 0.829 - 0.848, n = 1113 - 1228 species, P < 0.001). To increase the robustness of display scores, we only included species that were scored by at least two observers, and the maximum difference between scores was 2. Median scores are given for each species.

Inter-sexual resource sharing:

We collected verbal descriptions of territorial behaviour, and whether the birds fed on or away from the territory, and scored these descriptions on a three point scale: (0) males and females don't share resources and they feed away from their breeding territory; (1) males and females share resources on their territory only during the breeding season; (2) males and females share resources on their territory all year round. Again, scores were produced independently of each other, and blindly with regard to species name and other information in the data set. The scores were consistent among observers (r_S = 0.628 - 0.674, n = 1454 - 1629 species, P < 0.001). To increase the robustness of these scores, we only included species that were scored by at least two observers and the maximum difference between scores was 1. Median scores are given for each species.

Taxonomy and systematics:

Taxonomy and systematics follows Monroe and Sibley (1997).

Project Personnel: Akif Erdogan, Alison Meredith, Alejandro Serrano, Aron Székely, Tamas Székely Jr. Rene van Dijk and Hazel Watson contributed in data collection.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Status

Latest update: 31 January 2007

Latest Archive date: n/a

Metadata status: 31 January 2007, metadata is current

Data verification: Data quality has been carefully checked prior to our analyses of avian SSD as described in class V, section B below.

B. Accessibility

Storage location and medium: Copies of the latest version of the data file are being stored on all authors' personal computers in Microsoft Excel format.

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Copyright restrictions: None.

Proprietary restrictions: None.

Costs: None, the authors believe that scientific data should be free for scientific use.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data Set File

Identity: avian_ssd_jan07.txt

Size: 154,529 records, not including header row.

Format and storage mode: ASCII text, tab delimited, not compressed.

Header information: Headers describe the content of each column. We use the following abbreviations: M – male, F – female, N – sample size. Words and abbreviations are separated by underscores. Headers included are as follows: Family, Species_number, Species_name, English_name, subspecies, M_mass, M_mass_N, F_mass, F_mass_N, Unsexed_mass, Unsexed_mass_N, M_wing, M_wing_N, F_wing, F_wing_N, Unsexed_wing, Unsexed_wing_N, M_tarsus, M_tarsus_N, F_tarsus, F_tarsus_N, Unsexed_tarsus, Unsexed_tarsus_N, M_bill, M_bill_N, F_bill, F_bill_N, Unsexed_bill, Unsexed_bill_N, M_tail, M_tail_N, F_tail, F_tail_N, Unsexed_tail, Unsexed_tail_N, Clutch_size, Egg_mass, Mating_system, Display, Resource, References. See section B below for more detailed descriptions of the column contents.

Alphanumeric attributes: Mixed.

Special characters/fields: If no information is available for a given record, this is indicated by -999.

Authentication procedures: Sums for the numeric columns: Family = 367 034, Species_number = 18 465 081, M_mass = 286 290.6, M_mass_N = -1 618 267, F_mass = 51 506, F_mass_N = -1 740 296, Unsexed_mass = -2 537 689.736, Unsexed_mass_N = -3 369 508, M_wing = -322 790.11, M_wing_N = -1 232 547, F_wing = -361 303.41, F_wing_N = -1 283 159.6, Unsexed_wing = -3 626 834.77, Unsexed_wing_N = -3 680 551, M_tarsus = -1 129 931, M_tarsus_N = -1 529 610, F_tarsus = -1 173 399.98, F_tarsus_N = -1 584 574, Unsexed_tarsus = -3 585 852.42, Unsexed_tarsus_N = -3 635 205, M_bill = -1 027 849.16, M_bill_N = -1 416 995, F_bill = -1 073 102.09, F_bill_N = -1 470 093.1, Unsexed_bill = -3 611 359.545, Unsexed_bill_N = -3 641 213, M_tail = -1 156 761.2, M_tail_N = -1 404 542, F_tail = -1 207 805.7, F_tail_N = -1 454 685, Unsexed_tail = -3 606 677.4, Unsexed_tail_N = -3 658 091, Clutch_size = -1 367 375.305, Egg_mass = -1 108 130.235, Mating_system = -2 545 740, Display = -2 545 733, Resource = -2 191 472.

B. Variable definitions

Variable name	*Variable definition*	*Units*	*Storage type*	*Range numeric values*	*Missing value codes*
Family	Numbering of families according to the listing of all bird families in Monroe and Sibley (1997). See below for family names for each number.	n/a	Integer	1–146	n/a
Species_number	Species number according to the systematic order of all species listed by Monroe and Sibley (1997)	n/a	Integer	1–9702	n/a
Species name	Scientific species name (Genus species)	n/a	Character	n/a	n/a
English_name	Common name, according to Monroe and Sibley (1997)	n/a	Character	n/a	n/a
Subspecies	Name of the subspecies from which data on body size are given, in cases when this has been specifically stated by source. Note that in such cases, only data from this subspecies are included also for other morphometric variables.	n/a	Character	n/a	-999
M_mass	Body mass of males	grams	Floating point	2–115000	-999
M_mass_N	Sample size for male body mass data	n/a	Integer	1–6797	-999
F_mass	Body mass of females	grams	Floating point	2–100000	-999
F_mass_N	Sample size for female body mass data	n/a	Integer	1–3566	-999
Unsexed_mass	Body mass of unsexed birds	grams	Floating point	2.9–11350	-999
Unsexed_mass_N	Sample size for body mass data of unsexed birds	n/a	Integer	1–2589	-999
M_wing	Wing length of males	mm	Floating point	9–772	-999
M_wing_N	Sample size for male wing length data	n/a	Integer	1–1398	-999
F_wing	Wing length of females	mm	Floating point	38–798	-999
F_wing_N	Sample size for female wing length data	n/a	Integer	1–1463	-999
Unsexed_wing	Wing length of unsexed birds	mm	Floating point	49–900	-999
Unsexed_wing_N	Sample size for wing length data of unsexed birds	n/a	Integer	3–265	-999
M_tarsus	Tarsus length of males	mm	Floating point	2–426	-999
M_tarsus_N	Sample size for male tarsus length data	n/a	Integer	1–1130	-999
F_tarsus	Tarsus length of females	mm	Floating point	5–441	-999
F_tarsus_N	Sample size for female tarsus length data	n/a	Integer	1–744	-999
Unsexed_tarsus	Tarsus length of unsexed birds	mm	Floating point	9–450	-999
Unsexed_tarsus_N	Sample size for tarsus length data of unsexed birds	n/a	Integer	1–317	-999
M_bill	Bill length of males	mm	Floating point	3.6–409	-999
M_bill_N	Sample size for male bill length data	n/a	Integer	1–1139	-999
F_bill	Bill length of females	mm	Floating point	3.6–328	-999
F_bill_N	Sample size for female bill length data	n/a	Integer	1–765	-999
Unsexed_bill	Bill length of unsexed birds	mm	Floating point	6–176	-999
Unsexed_bill_N	Sample size for bill length data of unsexed birds	n/a	Integer	1–315	-999
M_tail	Tail length of males	mm	Floating point	17.3–762	-999
M_tail_N	Sample size for male tail length data	n/a	Integer	1–1029	-999
F_tail	Tail length of females	mm	Floating point	15.6–647.5	-999
F_tail_N	Sample size for female tail length data	n/a	Integer	1–762	-999
Unsexed_tail	Tail length of unsexed birds	mm	Floating point	29.6–300	-999
Unsexed_tail_N	Sample size for tail length data of unsexed birds	n/a	Integer	2–202	-999
Clutch_size	Average number of eggs produced per clutch, or the midpoints of ranges if averages were not available	n/a	Floating point	1–18.6	-999
Egg_mass	The average weight of a freshly laid egg	grams	Floating point	0.3–1500	-999
Mating_System	Scores of mating system. See section Class II B for definitions.	n/a	Integer	1–5	-999
Display	Scores of mating display agility. See section Class II B for definitions.	n/a	Integer	1–5	-999
Resource	Scores of territoriality and between-mate resource sharing. See section Class II B for definitions.	n/a	Integer	0–2	-999
References	Index numbers referring to sources of data for each species according to list of references given in section F below.	n/a	Comma delimited integers	1–89	n/a

<u>List of indexed bird families:</u> 1 Struthionidae, 3 Casuariidae, 4 Apterygidae, 5 Tinamidae, 6 Cracidae, 7 Megapodiidae, 8 Phasianidae, 9 Numididae, 10 Odontophoridae, 12 Anseranatidae, 13 Dendrocygnidae, 14 Anatidae, 15 Turnicidae, 16 Indicatoridae, 17 Picidae, 19 Lybiidae, 20 Ramphastidae, 21 Galbulidae, 22 Bucconidae, 23 Bucerotidae, 24 Bucorvidae, 25 Upupidae, 26 Phoeniculidae, 27 Rhinopomastidae, 28 Trogonidae, 29 Coraciidae,

32 Momotidae, 34 Alcedinidae, 35 Halcyonidae, 36 Cerylidae, 37 Meropidae, 38 Coliidae, 39 Cuculidae, 40 Centropidae, 41 Coccyzidae, 43 Crotophagidae, 44 Neomorphidae, 45 Psittacidae, 46 Apodidae, 48 Trochilidae, 49 Musophagidae, 50 Tytonidae, 51 Strigidae, 52 Aegothelidae, 53 Podargidae, 56 Nyctibiidae, 57 Eurostopodidae, 58 Caprimulgidae, 60 Columbidae, 61 Eurypygidae, 62 Otididae, 63 Gruidae, 64 Aramidae, 65 Heliornithidae, 69 Rallidae, 71 Pteroclidae, 72 Thinocoridae, 73 Pedionomidae, 74 Scolopacidae, 75 Rostratulidae, 76 Jacanidae, 77 Chionidae, 78 Pluvianellidae, 79 Burhinidae, 80 Charadriidae, 81 Glareolidae, 82 Laridae, 83 Accipitridae, 84 Sagittariidae, 85 Falconidae, 86 Podicipedidae, 87 Phaethontidae, 88 Sulidae, 89 Anhingidae, 90 Phalacrocoracidae, 91 Ardeidae, 92 Scopidae, 93 Phoenicopteridae, 94 Threskiornithidae, 95 Pelecanidae, 96 Ciconiidae, 97 Fregatidae, 98 Spheniscidae, 99 Gaviidae, 100 Procellariidae, 101 Acanthisittidae, 102 Pittidae, 103 Eurylaimidae, 105 Tyrannidae, 106 Thamnophilidae, 107 Furnariidae, 108 Formicariidae, 111 Climacteridae, 112 Menuridae, 113 Ptilonorhynchidae, 114 Maluridae, 115 Meliphagidae, 116 Pardalotidae, 117 Petroicidae, 119 Orthonychidae, 120 Pomatostomidae, 121 Laniidae, 122 Vireonidae, 123 Corvidae, 125 Picathartidae, 126 Bombycillidae, 127 Cinclidae, 128 Muscicapidae, 129 Sturnidae, 130 Sittidae, 131 Certhiidae, 132 Paridae, 133 Aegithalidae, 134 Hirundinidae, 135 Regulidae, 136 Pycnonotidae, 137 Hypocoliidae, 138 Cisticolidae, 139 Zosteropidae, 140 Sylviidae, 141 Alaudidae, 142 Nectariniidae, 143 Melanocharitidae, 145 Passeridae, 146 Fringillidae.

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Data acquisition

Data forms: n/a

Location of completed data forms: n/a

B. Quality assurance/quality control procedures: Data were entered directly into computer files, and were regularly checked for typographic errors during this process. Data from Dunn et al. (2001) were entered first, but changed if they deviated from our sources (see above). Any considerable differences between these two data sources would lead to an extra check of the values in question. After completion, biometric data for the two sexes were plotted against each other to search for outliers. We checked potential outliers in the source and changed them if errors appeared. After calculating sexual size dimorphism in all five biometric variables (ln male size – ln female size), we checked the 10 most extreme values in either direction for typographic errors. If a data point was expected to be wrong in the primary source, we checked it against other sources and changed the data point if necessary. Two presumed typographical errors were detected in this way in Birds of Africa (Fry et al. 1988, Fry and Keith 2000). First, male tail length in *Dendropicos elachus* was clearly erroneous when compared to the measure given for females (436.2 mm and 38.3 mm, respectively), and we used 36.2 for males. Second, for the species *Nectarinia habessinica*, the tarsus length of males seemed unrealistically long compared with that of females, and we used the measurements given by Cheke and Mann (2001) instead.

C. Related material: n/a

D. Computer programs and data processing algorithms: n/a

E. Archiving: n/a

F. Publications and results:

Reference list for data set: References are given as indexed values in accordance with the following reference list.

Reference number	Citation
1	Dunn, P. O., Whittingham, L. A. and Pitcher, T. E. 2001. Mating system, sperm competition, and the evolution of sexual dimorphism in birds. Evolution **55**:161-175.
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Publications citing the data set: Although more papers based on this data set are being prepared, the complete data set has so far only been used in the following publication:

Székely, T., T. Lislevand and J. Figuerola. *In press.* Sexual size dimorphism in birds. *In* Blanckenhorn, W. D. Fairbairn and T. Székely, editors, Sex, Size and Gender Roles. Oxford University Press, Oxford.

G. History of data set usage:

Data request history: Prof. G. Högstedt, University of Bergen, Norway, requested usage of body mass data for a study on avian plumage coloration (November 2006).

H. Data set update history

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