

UROPYGIAL GLAND SIZE AND AVIAN HABITAT

Diego Montalti^{1,2} & Alfredo Salibián³

¹Cátedra de Ornitología, Facultad de Ciencias Naturales y Museo,
Universidad Nacional de La Plata, Paseo del Bosque, 1900-La Plata, Argentina.

E-mail: dmontalti@arnet.com.ar

²Departamento de Biología, Aves, Instituto Antártico Argentino, Cerrito 1248,
1010-Buenos Aires, Argentina.

³CIC Buenos Aires and Universidad Nacional de Luján (Programa de Ecofisiología Aplicada),
6700-Luján (B), Argentina.

Resumen. El papel fisiológico de la glándula uropigia es hasta ahora una controversia. Algunos autores afirman que su función podría estar estrechamente vinculada con las propiedades hidrofóbicas de su secreción, que puede ser esencial para impermeabilizar el plumaje. Por consiguiente podría esperarse que el grado de desarrollo de esta glándula debe ser mayor en aves acuáticas que en especies terrestres. Con el objeto de validar esta hipótesis, se determinó el peso de la glándula (GW) relativo al peso corporal (BW) expresando los resultados como porcentajes (GW x 100/BW). Se analizaron los datos de 1164 individuos de 126 especies de aves adultas de 49 familias. Los resultados mostraron la ausencia de una clara correlación entre el índice calculado y el grado de contacto de las aves con el agua. No se observó correlación filogenética derivada de la presencia de la glándula uropigia.

Abstract. The physiological role of the uropygial gland is still controversial. Certain authors state that its function could be closely connected to the hydrophobic properties of its secretion, that may be essential for plumage waterproofing. Therefore, it could be hypothesized that the degree of this gland's development should be greater in aquatic birds than in terrestrial species. In order to validate that hypothesis, gland's mass (GW) relative to body weight (BW) was determined, expressing the results as percentages (GW x 100/BW). Data of 1164 adult individuals from 126 bird species from 49 families were analysed. Results showed the absence of a clear cut correlation between the calculated index and the degree of birds' contact with water. No phylogenetic correlation was observed derived from the presence of the uropygial gland. Accepted 15 June 2000.

Key words: Uropygial gland, habitat, aquatic birds, terrestrial birds.

INTRODUCTION

The uropygial gland, may be considered as the only organized tegumentary structure of external secretion typical of birds, is always found in embryonic stages, while in adults of some species it may be vestigial or absent (Rheidae, Psittacidae and Columbidae) (Johnston 1988). It is a holocrine gland that secretes a complex and variable mixture of substances formed greatly of aliphatic

monoester waxes, formed of fatty acids (with various degree of methyl branching) and monohydroxy wax-alcohols. However, some types of diester waxes containing hydroxyfatty acids and/or alkane-diols exist in the secretions of the uropygial gland of some groups of birds (Jacob & Ziswiler 1982, Downing 1986, Jacob 1992) and is highly specialized in lipid synthesis (Kolattukudy & Rogers 1978, Urich 1994).

Morphological descriptions of the gland

of different taxa and systematic classifications based on its morphology and chemical nature of secretory lipids have been reported (Jacob & Ziswiler 1982, Johnston 1988). Information on the uropygial gland's histology, secretion chemistry, and possible physiological functions has been recorded (Elder 1954, Lucas & Stettenheim 1972, Jacob & Ziswiler 1982, Montalti *et al.* 1994). It is interesting to mention that Jacob *et al.* (1979) demonstrated sexual differences in the chemical composition of the secretion in domestic ducks. The extirpation of the uropygial gland did not reveal any serious consequence for the survival of pigeons (Montalti *et al.* 1999), hens, and passerine birds (Jacob 1976).

The physiological function of this gland has not been studied extensively. Many workers hold that this gland's function is closely connected with the hydrophobic properties of its secretion, which would have an essential role in plumage waterproofing. It is also possible that the gland could play a role in plumage hygiene against microflora and/or in supplying provitamin D and repository and excretory function for several pesticides and pollutants (Johnston 1975, 1976, 1978, Jacob & Ziswiler 1982, Quay 1986, Kozulin & Pavluschick 1993, Pilastro *et al.* 1993, Jacob *et al.* 1997, Gutiérrez *et al.* 1998, Bandyopadhyay & Bhattacharyya 1996, 1999). We undertook this study in order to check this point of view. Our hypothesis was that adult birds' gland size, considering its weight relative to the body weight, should be related to the bird's habitat, being relatively greater in species that are in permanent or temporary contact with water than in terrestrial species.

MATERIALS AND METHODS

Data used in this work came from two sources. Some of them were taken from Jacob & Ziswiler (1982) and Johnston (1988). Most of them came from measurements carried out

at our laboratory between 1985 and 1995. In the latter case, birds were captured in different places of the Buenos Aires province, Argentina; penguins (Spheniscidae), petrels (Procelariidae and Hydrobatidae), cormorants (Phalacrocoracidae), sheathbills (Chionidae) and skuas (Stercorariidae) came from King George Island (South Shetland Islands) and from Laurie Island (South Orkney Islands), Antarctica. A few samples were provided by the La Plata Zoo.

Some 1164 individuals from 126 species and 49 families were studied in total. Body weight was determined in the field or at the laboratory, using a dynamometer balance (± 1 g accuracy); glands were removed according to the technique developed by Montalti *et al.* (1998) and weighed with an electronic balance (± 0.01 g accuracy). These values were used to calculate the gland's mass as percentage in relation to body weight ($GW \times 100/BW$) for each one of the considered species. Following Johnston's procedure (1988), data were grouped in families and a mean gland weight (as %) for each species was calculated. When the number of data was higher than two, results were expressed as means \pm SD; otherwise individual values were shown. Data were evaluated statistically by one-way analysis of variance and the Tukey test.

RESULTS AND DISCUSSION

The Appendix shows the results ordered according to the systematic sequence of Morony *et al.* (1975). We found the largest mean relative gland weight in the Sternidae (*Sterna trudeani*, mean = 0.522), Podicipedidae (*Podilymbus podiceps*, 0.418–0.556) and Procelariidae (*Daption capense*, mean = 0.426). These findings are coincident with those of Jacob & Ziswiler (1982) and Johnston (1988) who also found the largest gland's weight in other species of the same families.

Among the Passeriformes, the greatest

relative weights were recorded in the Furnariidae (*Phacellodomus striaticollis*, mean = 0.363), Tyrannidae (*Serpophaga subcristata*, mean = 0.359), and Emberizidae (*Poospiza nigrorufa*, 0.280–0.320). Kennedy (1971) and Jacob & Ziswiler (1982) recorded the largest value in Passeriformes in Troglodytidae (*Troglodytes troglodytes*, 0.561 and 0.580) whereas, in a larger sample of *Troglodytes aedon*, we found a much lower value (mean = 0.245).

The smallest glands proportional to body weight were found in Ardeidae (*Bubulcus ibis*, mean = 0.014), and in Columbidae (*Columba picazuro*, mean = 0.016). Other authors (Kennedy 1971, Jacob & Ziswiler 1982, Johnston 1988) have reported similar results in Columbidae. The small size of the gland in these families may be attributed to the presence of the powder down; it is known that some birds such as herons, pigeons and kagus possess a rudimentary preen gland whose function may be fulfilled by powder down (Jacob 1976). Thus, the well developed powder down production may explain their reduced uropygial glands or absence of it (Johnston 1988).

In this study, it came out that there was no clear cut correlation between gland's size and the bird's exposure to water. It is accepted that species that plunge into the water to capture their prey would require larger glands than species that pick their prey from the water surface, almost without contact with water (see Jacob & Ziswiler 1982). However, the relative gland weight appeared without a clear relationship with the degree of aquaticity of the considered species. In spite of their condition of being fully aquatic species, the relative size of Sternidae resulted one of the largest among the species we studied; similar findings were reported by Johnston (1988) for *S. albifrons*.

On the other hand, birds living in aquatic environments not always have a more developed gland than non-aquatic birds. If we

compare the size of glands of aquatic vs landbirds, it will come out that both show comparable values in spite of their different habitats; for instance, *Anas georgica* (mean = 0.306) vs *Guira guira* (mean = 0.296); *Pygoscelis adeliae* (mean = 0.159) vs *Colaptes campestris* (mean = 0.174).

When comparing the gland size among landbird species, we found great variability. That is the case of fully terrestrial species as *Zonotrichia capensis* (mean = 0.198), *Milvago chilensis* (mean = 0.143), *Athene cunicularia* (mean = 0.090) and *Zenaida auricularia* (mean = 0.026). On the other hand, it is interesting that if we compare the glands' size of aquatic species, but of dissimilar degree of aquaticity, it can be noted the existence of peculiar differences. *Pygoscelis papua*, which is a pursuit diving species, has a gland size of 0.132 %, while in *Daption capense*, a surface filterer bird, the size is 0.426 %. The size of the glands of these seabirds seems to be in the opposite direction of the expected values, i.e., the gland size of *P. papua* might be larger than the gland of *D. capense* because their feeding behaviour involves a different degree of contact with water. A similar trend is observed when the comparison between freshwater species is done; that is the case of *Fulica rufifrons* (mean = 0.168) and *Anas versicolor* (mean = 0.342).

Several authors have reported differences in relative gland weights, attributing them to seasonal variations (Kennedy 1971), habitat (Jacob & Ziswiler 1982), body weight (Johnston 1979), individual variation, and sex (Johnston 1988). In our case, no difference was found in the gland relative size between males and females.

Analysis of birds' phylogenetic classification (according to Morony *et al.* 1975) shows that despite the fact that the number of our samples may be considered small, the trend of the development of the gland was independent from the lineage of the birds. Thus,

the uropygial gland is present in birds phylogenetically distant (Tinamidae-Hirundinidae) or, on the contrary, absent in phylogenetically close taxa (some Psittacidae and Columbidae).

In summary, if we assume that the gland's mass constitutes a valid parameter to quantify its degree of gland development, our results indicate that the physiological role of the gland does not depend upon gland mass. Chemical composition of the secretion may be involved in this (Jacob 1978). The role could be more complex than a feather waterproofing function.

There is no evidence that glands of similar mass produce comparable quantities of secretion. Consequently, we cannot disregard the possibility that the degree of contact with water might rather be associated with adaptive changes in the composition of the secretion, involving the biosynthesis routes of the gland's lipids.

ACKNOWLEDGMENTS

This work was supported by grants from the Universidad Nacional de La Plata (Programa de Incentivos). D.M. is affiliated to the Cátedra de Fisiología Animal, FCNyM-UNLP.

REFERENCES

- Bandyopadhyay, A. & Bhattacharyya S. P. 1996. Influence of fowl uropygial gland and its secretory lipid components on the growth of skin surface bacteria of fowl. Indian J. Exp. Biol. 34:48–52.
- Bandyopadhyay, A. & S. P. Bhattacharyya. 1999. Influence of uropygial gland and its secretory components on the growth of skin surface fungi of fowl. Indian J. Exp. Biol. 37:1218–1222.
- Downing, D. T. 1986. Skin lipids, preen gland and scent gland lipids. Pp. 833–840 in Bereiter-Hahn J., A.G. Matoltsy & K.C. Parks (eds.), Biology of the integument, Vol. 2. New York.
- Elder, W. H. 1954. The oil gland of birds. Wilson Bull. 66: 6–31.
- Gutiérrez, A. M., D. Montalti, G. R. Reboreda, A. Salibián, & A. Catalá. 1998. Lindane distribution and fatty acid profiles of uropygial gland and liver of *Columba livia* after pesticide treatment. Pestic. Biochem. Physiol. 59: 137–141.
- Jacob, J. 1976. Bird waxes. Pp. 93–146 in Kolattukudy, P. E. (ed.). Chemistry and biochemistry of natural waxes. Elsevier, Amsterdam.
- Jacob, J. 1992. Systematics and the analysis of integumental lipids. Bull. Br. Ornithol. Club 112A: 159–167.
- Jacob, J., J. Balthazart, & E. Schoffeniels. 1979. Sex differences in the chemical composition of uropygial gland waxes in domestic ducks. Biochem. Syst. Ecol. 7: 149–153.
- Jacob, J., U. Eigene, U. Hoppe. 1997. The structure of preen gland waxes from Pelecaniform birds containing 3,7-dimethyloctan-1-ol - an active ingredient against dermatophytes. Z. Naturforsch Sect C-A J. Biosci. 52: 114–123.
- Jacob, J., & V. Ziswiler. 1982. The uropygial gland. Pp. 199–324 in Farner, D. S., J. R. King, & K. C. Parkes (eds.), Avian biology, Vol. 6. Academic Press, New York.
- Johnston, D. W. 1975. Organochlorine pesticide residues in small migratory birds, 1964–73. Pestic. Monit. J. 9: 79–88.
- Johnston, D. W. 1976. Organochlorine pesticide residues in uropygial glands and adipose tissue of wild birds. Bull. Environ. Contam. Toxicol. 16: 149–155.
- Johnston, D. W. 1978. Organochlorine pesticide residues in Florida birds of prey, 1969–76. Pestic. Monit. J. 12:8–15.
- Johnston, D. W. 1988. A morphological atlas of the avian uropygial gland. Bull. Br. Mus. (Nat. Hist.) Zool. 54: 199–259.
- Kolattukudy, P. E., & L. Rogers. 1978. Biosynthesis of fatty alcohols, alkane-1,2-diols and wax esters in particulate preparations from the uropygial glands of white-crowned sparrows (*Zonotrichia leucophrys*). Arch. Biochem. Biophys. 191: 244–258.
- Kozulin, A., & T. Pavluschick. 1993. Content of heavy metals in tissues of mallards *Anas platyrhynchos* wintering in polluted and unpolluted habitats. Acta Ornithol. 28: 55–60.

- Lucas, A. M., & P. R. Stettenheim. 1972. Uropygial gland. Pp. 613–626 in Agriculture handbook 362. Avian anatomy project, Poultry research branch, Animal science research division, Agricultural research service, U. S. Department of agriculture, Washington, D.C..
- Montalti D, A. M. Gutiérrez, & A. Salibián. 1998. Técnica quirúrgica para la ablación de la glándula uropigia en la paloma casera *Columba livia*. Rev. Bras. Biol. 58: 193–196.
- Montalti D, A. M. Gutiérrez, G. R. Reboreda, & A. Salibián. 1999. Ablación de la glándula uropigia y sobrevida de *Columba livia*. Boll. Mus. civ. Stor. nat. Venezia 50: –.
- Montalti, D, M. A. Quiroga, A. R. Massone, J. R. Idiart, & A. Salibian. 1994. Estudios histocímicos y lectinhistoquímicos de la glándula uropigia de *Columba livia* (Aves,Columbidae). Congr. Arg. Cs. Vet, Buenos Aires 7 (Resumenes): 446.
- Morony, J. J., W. J. Bock, & J. Farrand. 1975. Reference list of the birds of the world. Am. Mus. Nat. Hist. Spec. Publ., New York.
- Pilastro, A., L. Congiu, L. Tallandini, & M. Turchetto. 1993. The use of bird feathers for the monitoring of cadmium pollution. Arch. Environ. Contam. Toxicol. 24: 355–358.
- Quay, W. B. 1986. Uropygial gland. Pp. 248–254 in Bereiter-Hahn J, A. G. Matoltsy & K. C. Parks (eds.). Biology of the integument, Vol. 2. New York.
- Urich, K. 1994. Comparative animal biochemistry. Springer Verlag, Berlin.

APPENDIX. Uropygial gland weight relative to body mass (gland weight x 100/ body weight). Data as percentage (mean ± SD). Species listed according to Morony *et al.*(1975).

FAMILY/Especies ^{1,2}	Mean	SD	n ³
TINAMIDAE			
<i>Rhynchotus rufescens</i>	0.080	0.017	6
<i>Nothura maculosa</i>	0.141	0.042	41
SPHENISCIDAE (A)			
<i>Pygoscelis papua</i>	0.132	0.015	10
<i>Pygoscelis adeliae</i>	0.159	0.042	16
<i>Pygoscelis antarctica</i>	0.217	0.070	6
GAVIIDAE (A)			
<i>Gavia stellata</i> **	0.190	0.016	3
<i>Gavia immer</i> **	0.103	0.009	3
PODICIPEDIDAE (A)			
<i>Podilymbus podiceps</i>	0.418-0.556	—	2
<i>Rollandia rolland</i>	0.428	0.107	10
PROCELLARIIDAE (A)			
<i>Macronectes giganteus</i>	0.191-0.437	—	2
<i>Daption capense</i>	0.426	0.047	5
<i>Halobaena caerulea</i>	0.212-0.332	—	2
HYDROBATIDAE (A)			
<i>Oceanites oceanicus</i>	0.445	0.055	16
<i>Fregetta tropica</i>	0.459	0.079	5
PELECANIDAE (A)			
<i>Pelecanus occidentalis</i> **	0.373	0.045	3
FREGATIDAE (A)			
<i>Fregata magnificens</i> **	0.067	0.005	3
PHALACROCORACIDAE (A)			
<i>Phalacrocorax olivaceus</i>	0.279	0.066	6

APPENDIX. Continuation.

FAMILY/Especies ^{1,2}	Mean	SD	n ³
<i>Phalacrocorax bransfieldensis</i>	0.154	0.041	3
<i>Phalacrocorax georgianus</i>	0.191-0.194	—	2
ANHINGIDAE (A)			
<i>Anhinga anhinga</i> **	0.152	0.017	5
SULIDAE (A)			
<i>Sula bassana</i> *	0.350	—	2
ARDEIDAE			
<i>Syrigma sibilatrix</i>	0.025	0.006	4
<i>Egretta alba</i>	0.029	0.006	7
<i>Egretta thula</i>	0.029	0.013	8
<i>Bubulcus ibis</i>	0.014	0.007	3
<i>Nycticorax nycticorax</i>	0.031-0.041	—	2
CICONIDAE			
<i>Ciconia maguari</i>	0.051-0.074	—	2
<i>Ciconia ciconia</i>	0.077-0.082	—	2
THRESKIORNITHIDAE			
<i>Plegadis chihi</i>	0.208	0.043	31
<i>Platalea ajaja</i>	0.148-0.190	—	2
PHOENICOPTERIDAE			
<i>Phoenicopterus chilensis</i>	0.181	0.043	12
ANHIMIDAE			
<i>Chauna torquata</i>	0.063	0.016	3
ANATIDAE (A)			
<i>Dendrocygna viduata</i>	0.263	0.035	8
<i>Cygnus melanocorypha</i>	0.152	0.012	3
<i>Coscoroba coscoroba</i>	0.234	0.057	4
<i>Chloephaga picta</i>	0.063-0.095	—	2
<i>Cairina moschata</i>	0.242	0.065	5
<i>Anas flavirostris</i>	0.382	0.066	8
<i>Anas georgica</i>	0.306	0.120	9
<i>Anas versicolor</i>	0.342	0.108	5
<i>Netta peposaca</i>	0.408	0.134	4
CATHARTIDAE			
<i>Coragyps atratus</i> **	0.043	0.004	4
ACCIPITRIDAE			
<i>Elanus leucurus</i>	0.094	0.015	3
<i>Rostrhamus sociabilis</i>	0.097	0.020	11
<i>Circus buffoni</i>	0.065	0.013	4
<i>Buteo magnirostris</i>	0.044	0.011	4
FALCONIDAE			
<i>Polyborus plancus</i>	0.060	0.018	6
<i>Milvago chimango</i>	0.143	0.033	17
<i>Falco sparverius</i>	0.082	0.022	6
PHASIANIDAE			
<i>Gallus gallus</i>	0.094	0.041	3

APPENDIX. Continuation.

FAMILY/Especies ^{1,2}	Mean	SD	n ³
ARAMIDAE			
<i>Aramus guarauna</i>	0.141	0.020	4
RALLIDAE (A)			
<i>Aramides ypecaha</i>	0.114	0.020	6
<i>Pardirallus maculatus</i>	0.294-0.342	—	2
<i>Pardirallus sanguinolentus</i>	0.281-0.316	—	2
<i>Gallinula chloropus</i>	0.222	0.033	6
<i>Gallinula melanops</i>	0.296	0.091	4
<i>Fulica armillata</i>	0.111-0.219	—	2
<i>Fulica rufifrons</i>	0.168	0.048	4
GRUIDAE			
<i>Grus canadensis</i> **	0.045	0.009	4
JACANIDAE (A)			
<i>Jacana jacana</i>	0.157	0.032	6
ROSTRATULIDAE			
<i>Nycticryphes semicollaris</i>	0.191	0.017	3
RECURVIROSTRIDAE			
<i>Himantopus himantopus</i>	0.088	0.006	4
CHARADRIIDAE			
<i>Vanellus chilensis</i>	0.096	0.023	51
SCOLOPACIDAE			
<i>Tringa flavipes</i>	0.231	0.031	8
<i>Calidris fuscicollis</i>	0.251	0.036	22
CHIONIDAE			
<i>Chionis alba</i>	0.202	0.029	6
STERCORARIIDAE (A)			
<i>Cathartes maccormicki</i>	0.211	0.053	17
<i>Cathartes antarctica</i>	0.172	0.049	35
LARIDAE (A)			
<i>Larus dominicanus</i>	0.174	0.058	13
<i>Larus cirrocephalus</i>	0.232	0.043	6
<i>Larus maculipennis</i>	0.225	0.042	23
STERNIDAE (A)			
<i>Sterna trudeaui</i>	0.522	0.031	3
RHYNCHOPIDAE (A)			
<i>Rynchops niger</i> **	0.200	—	6
ALCIDAE (A)			
<i>Uria aalgae</i> *	0.170	—	2
<i>Alca torda</i> *	0.220	—	3
COLUMBIDAE			
<i>Columba livia</i>	0.026	0.012	50
<i>Columba picazuro</i>	0.016	0.005	9
<i>Columba maculosa</i>	0.022	0.006	7
<i>Zenaida auriculata</i>	0.026	0.010	26
<i>Columbina picui</i>	0.069	0.016	5

APPENDIX. Continuation.

FAMILY/Especies ^{1,2}	Mean	SD	n ³
PSITTACIDAE			
<i>Melopsittacus undulatus</i>	0.207	0.023	5
<i>Ara macao</i>	0.057-0.097	—	2
<i>Nandayus nenday</i>	0.084	0.004	3
<i>Cyanoliseus patagonus</i>	0.094-0.117	—	2
<i>Myiopsitta monachus</i>	0.094	0.033	12
CUCULIDAE			
<i>Guira guira</i>	0.296	0.111	35
TYTONIDAE			
<i>Tyto alba</i>	0.121	0.033	3
STRIGIDAE			
<i>Asio flammeus</i>	0.068-0.089	—	2
<i>Athene cunicularia</i>	0.090	0.028	10
<i>Bubo virginianus</i> **	0.038	0.004	4
APODIDAE			
<i>Apus apus</i> *	0.050	—	7
TROCHILIDAE			
<i>Chlorostilbon aureoventris</i>	0.286-0.288	—	2
ALCEDINIDAE (A)			
<i>Chloroceryle americana</i>	0.415-0.510	—	2
RAMPHASTIDAE			
<i>Ramphastos toco</i>	0.065-0.071	—	2
PICIDAE			
<i>Colaptes campestroides</i>	0.174	0.021	10
<i>Colaptes melanolaemus</i>	0.108	0.027	11
<i>Melanerpes carolinus</i> **	0.117	0.02	3
FURNARIIDAE			
<i>Cinclodes fuscus</i>	0.223	0.033	11
<i>Furnarius rufus</i>	0.125	0.045	29
<i>Phacellodomus striaticollis</i>	0.363	0.083	5
<i>Schoeniophylax phryganophilus</i>	0.309	0.049	5
<i>Anumbius annumbi</i>	0.240	0.094	9
<i>Lessonia rufa</i>	0.121	0.020	3
TYRANNIDAE			
<i>Machetornis rixosus</i>	0.150	0.007	5
<i>Tyrannus savana</i>	0.103	0.032	19
<i>Tyrannus melancholicus</i>	0.104	0.045	8
<i>Pitangus sulphuratus</i>	0.124	0.037	25
<i>Pyrocephalus rubinus</i>	0.143	0.046	7
<i>Serpophaga subcristata</i>	0.359	0.183	3
<i>Serpophaga nigricans</i>	0.248	0.083	4
<i>Satrapa icterophrys</i>	0.089-0.178	—	2
<i>Xolmis coronata</i>	0.053-0.083	—	2
<i>Hymenops perspicillatus</i>	0.161	0.022	4
PHYTOTOMIDAE			
<i>Phytotoma rutila</i>	0.111	0.023	10

APPENDIX. Continuation.

FAMILY/Especies ^{1,2}	Mean	SD	n ³
HIRUNDINIDAE			
<i>Phaeoprogne tapera</i>	0.076	0.016	6
<i>Tachycineta leucorrhoa</i>	0.125	0.032	4
MOTACILIDAE			
<i>Anthus hellmayri</i>	0.257	0.043	3
TROGLODYTIIDAE			
<i>Troglodytes aedon</i>	0.245	0.067	13
POLIOPTILIDAE			
<i>Polioptila dumicola</i>	0.153	0.085	9
MIMIDAE			
<i>Mimus saturninus</i>	0.134	0.026	9
<i>Mimus triurus</i>	0.074	0.017	3
TURDIDAE			
<i>Turdus rufiventris</i>	0.129	0.027	3
<i>Turdus amaurochalinus</i>	0.064-0.093	—	2
<i>Turdus migratorius</i> **	0.100	0.014	3
EMBERIZIDAE			
<i>Sicalis flaveola</i>	0.101	0.028	5
<i>Zonotrichia capensis</i>	0.198	0.084	35
<i>Paroaria coronata</i>	0.093	0.022	4
<i>Poospiza nigrorufa</i>	0.278-0.323	—	2
<i>Donacospiza albifrons</i>	0.366-0.620	—	2
<i>Embernagra platensis</i>	0.275	0.079	26
<i>Cardinalis cardinalis</i> **	0.083	0.009	3
ICTERIDAE			
<i>Molothrus bonariensis</i>	0.116	0.042	6
<i>Molothrus badius</i>	0.262	0.076	27
<i>Molothrus rufoaxillaris</i>	0.143	0.012	3
<i>Icterus cayanensis</i>	0.140	0.013	3
<i>Agelaius thilius</i>	0.212	0.054	31
<i>Pseudoleistes virescens</i>	0.246	0.051	13
<i>Sturnella superciliaris</i>	0.242	0.056	27
FRINGILLIDAE			
<i>Carduelis magellanicus</i>	0.122	0.032	16
<i>Serinus canarius</i>	0.151-0.186	—	2
STURNIDAE			
<i>Sturnus vulgaris</i> **	0.117	0.009	3
CORVIDAE			
<i>Corvus corax</i> *	0.120	—	6
<i>Corvus corone</i> *	0.100	—	8
<i>Pica pica</i> *	0.090	—	5
<i>Cyanocitta cristata</i> **	0.127	0.052	3
PARIDAE			
<i>Parus major</i> *	0.140	—	12
<i>Parus ater</i> *	0.150	—	11

APPENDIX. Continuation.

FAMILY/Especies ^{1,2}	Mean	SD	n ³
AEGITHALIDAE <i>Aegithalos caudatus</i> *	0.210	—	2
ESTRILDIDAE <i>Padda oryzivora</i>	0.111-0.136	—	2
PLOCEIDAE <i>Passer domesticus</i>	0.171	0.061	22

¹(A) means aquatic bird.²Asterisks indicate the source of information: * = from Jacob & Ziswiler (1982), ** = from Johnston (1988).³n = number of specimens of each species.