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Nest humidity and egg water vapor conductance of archosaurs: Implications for nesting modes

Tanaka, Kohei

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Nest humidity and egg water vapor conductance of archosaurs:

Implications for nesting modes

by

Kohei Tanaka

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Abstract

Absolute nest humidity (P_{nest}) and egg water vapor conductance ($G_{\text{H}_2\text{O}}$) of 295 taxa of living archosaurs are analyzed to test if P_{nest} and $G_{\text{H}_2\text{O}}$ are correlated to nest types. P_{nest} is shown to be significantly higher in covered nest types than in non-covered nest types, likely because enclosed environments retain more humidity. Also, estimated P_{nest} of some waterbirds (e.g., grebes) with non-covered cup nests is high and comparable to that of covered nests, probably because the nest material is wet. Species that incubate eggs in humid nests are shown to have significantly higher $G_{\text{H}_2\text{O}}$ than those incubating in regular nests (less humid), and these differences in $G_{\text{H}_2\text{O}}$ between nester types prevent excess humidification or desiccation of the eggs. Therefore, P_{nest} and $G_{\text{H}_2\text{O}}$ of the eggs appear to be closely related to nesting types in archosaurs, the latter of which can potentially be used to infer nest types of extinct archosaurs.

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List of Abbreviations

A	Mean cross-sectional individual pore area (μm^2)
AIC	Akaike Information Criterion
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
A_p	Total pore area (mm^2)
α	Angular eccentricity [= arcos (L' / B')]
A_s	Surface area of egg (mm^2)
B	Maximum egg breadth (mm)
B'	Half of the maximum egg breadth (mm)
CI	Confidence interval
D	Pore density (n/mm^2)
$D_{\text{H}_2\text{O}}$	Diffusion coefficient of water vapor (cm^2/sec)
ΔP	Gradient between P_{nest} and P_a ($= P_{\text{nest}} - P_a$)
d.f.	Degree of freedom
Eq.	Equation
$G_{\text{H}_2\text{O}}$	Water vapor conductance ($\text{mgH}_2\text{O}/\text{day}/\text{Torr}$)
k	Conversion constant ($\text{sec mg}/\text{day}/\text{mol}$)
L	Maximum egg length (mm)
L'	Half of the maximum egg length (mm)
log	logarithm
L_s	Shell thickness (= pore length) (mm)
M	Egg mass (g)
$M_{\text{H}_2\text{O}}$	Rate of daily weight (= water) loss of egg ($\text{mgH}_2\text{O}/\text{day}$)
n	Sample size
N	Total number of pores (n/egg)
OLS	Ordinary least-squares
p	Probability for a hypothesis test
P_a	Absolute ambient humidity of the nesting habitat (Torr)
Pc ANCOVA	Phylogenetically-corrected ANCOVA (contra to non-pc ANOVA: non-phylogenetically corrected ANCOVA)
P_{egg}	Absolute egg humidity (= absolute water vapor pressure of the egg) (Torr)
PGLS	Phylogenetic generalized least-squares assumed Brownian motion process
P_{nest}	Absolute nest humidity (= absolute water vapor pressure of the nest) (Torr)
R	Universal gas constant ($\text{cm}^3 \text{Torr}/\text{mol}/\text{K}$)
r^2	Coefficient of determination
RegOU	Phylogenetic regression with Ornstein-Uhlenbeck process
ROM	Royal Ontario Museum, Toronto
SD	Standard deviation
T	Temperature ($^{\circ}\text{C}$)
T'	Absolute temperature (K)
T_a	Ambient air temperature of the nesting habitat ($^{\circ}\text{C}$)
T_{nest}	Nest temperature ($^{\circ}\text{C}$)
ZEC	Zelenitsky Egg Catalogue, the University of Calgary, Calgary

CHAPTER ONE: GENERAL INTRODUCTION

1.1 Introductory Statement

The nesting mode of archosaurs is extremely important for incubation and hatching success. Nests are designed to help regulate temperature and humidity, allow gas exchange (i.e., oxygen intake, carbon dioxide exhaust, and water vapor diffusion) for embryonic development, as well as protect eggs from depredation (Ar and Sidis, 2002; Hansell and Deeming, 2002). Regardless of the type of nest architecture and nesting habitat, eggs are incubated at an optimal incubation temperature (around 35 °C for birds and 30 °C for crocodilians: Drent, 1975; Ferguson, 1985; Webb, 1987) and lose a certain amount of water during incubation (10 to 23 % of initial egg mass: Ar and Rahn, 1980). Thus, nest architecture, nest microclimate (e.g., humidity, temperature), as well as physiological properties of the eggs are interrelated.

In this thesis, I investigate relationships between nest types and physical and physiological properties related to egg water loss during incubation of eggs of living archosaurs. Nest humidity (P_{nest} , Torr) is particularly important because it directly affects the water vapor conductance ($G_{\text{H}_2\text{O}}$, $\text{mgH}_2\text{O}/\text{day}/\text{Torr}$) of the egg, which helps regulate water loss from the eggs via the pores that pierce through the eggshell (Ar et al., 1974). Water vapor conductance is assumed to be higher in humid (covered) nests and lower in dry (open) nests so that water vapor loss during incubation is normal (Ar and Rahn, 1985), thus preventing excess humidification or desiccation of the eggs. Nest structure or nest type is generally not preserved in extinct archosaurs, although estimates of $G_{\text{H}_2\text{O}}$ for the eggs of extinct archosaurs have been widely used to predict their nest types/modes (Seymour, 1979; Williams et al., 1984; Sabath, 1991; Mou, 1992; Grigorescu et al., 1994; Mikhailov et al., 1994; Sahni et al., 1994; Antunes et al., 1998; Deeming, 2006; Jackson et al., 2008, 2010; Donaire and Lopez-Martinez, 2009; Grellet-Tinner et al., 2012), without verification of a relationship between nest type and egg water vapor conductance in living archosaurs. Thus, for this study, data from the eggs and nests of approximately 300 living archosaur species are analyzed statistically to test for relationships among nest microclimate (i.e., humidity), $G_{\text{H}_2\text{O}}$, and nest type. This study is significant in that it will determine if calculation of water

vapor conductance in the eggs of extinct archosaurs can be utilized to infer nest types or nesting mode.

1.2 Nesting Modes of Living Archosaurs

Living archosaurs (i.e., birds and crocodilians) build a variety of nest architectures in a variety of environments and climates, using a variety of incubation techniques or behaviors (Coombs, 1989; Hansell, 2000). Nest architectures include a simple scrape (e.g., Arctic Tern) to sophisticated dome and tube structure (e.g., weavers) (Hansell and Deeming, 2002). Most birds incubate eggs in non-covered nests (e.g., scrape, bed, plate, cup, dome, dome and tube, and burrow: Hansell, 2000) by using parent body heat (i.e., brooding). Among brooders, some are unique in that nests are generally composed of wet plant materials in aquatic environments (e.g., grebes, loons, jacanas, and black terns: Roberts, 1936; Bent, 1963; Bergman et al., 1970; Lomholt, 1976; Goodfellow, 1977; Terres, 1980; Davis et al., 1984; Sotherland et al., 1984; Storer and Nuechterlein, 1992; Dunn and Agro, 1995; McIntyre and Barr, 1997; Jenni and Mace, 1999; Muller and Storer, 1999). Although most waterbirds brood their eggs in nest cups, grebes are known to leave the nests and cover the eggs with nest material (e.g., Davis et al., 1984; Storer, 1992; Storer and Nuechterlein, 1992; Muller and Storer, 1999; Stout and Nuechterlein, 1999; Stedman, 2000; Prokop and Trnka, 2011). Megapodes (Family Megapodiidae) are also peculiar among birds as they do not brood their eggs, but rather build nests in which the eggs are covered with vegetation and sediment and use external heat sources for incubation (Jones et al., 1995; Booth and Jones, 2002). Megapode eggs are laid within an infilled hole in the ground or within a mound (i.e., a heap of nest materials) on the ground (Jones et al., 1995; Booth and Jones, 2002). Although adults may help regulate the temperature and humidity of nests through behaviors (Fleay, 1937; Frith, 1962; Seymour et al., 1986, 1987; Jones et al., 1995), eggs are incubated via solar radiation, geothermal activity, or microbial respiration (Booth and Jones, 2002). Crocodilians also have eggs that are covered by nesting material, either in mounds or infilled holes (e.g., Ferguson, 1985; Coombs, 1989; Brazaitis and Watanabe, 2011). Temperature and humidity are controlled in crocodilians, factors that are extremely important because they are determinants of embryonic development, sex determination, and hatching success (Ferguson, 1985). The diverse nest types and behaviors of archosaur

species allow them to breed in various environments, from aquatic to desert environments, to high montane and even polar regions (Carey, 1980a, 2002).

1.3 Reconstruction of Nesting Modes in Extinct Archosaurs and New Approaches in This Study

Nest types of extinct archosaurs (e.g., non-avian dinosaurs, extinct birds) have often been inferred based on estimates of water vapor conductance of their eggs derived from egg size and total eggshell porosity (Seymour, 1979; Williams et al., 1984; Sabath, 1991; Mou, 1992; Grigorescu et al., 1994; Mikhailov et al., 1994; Sahni et al., 1994; Antunes et al., 1998; Deeming, 2006; Jackson et al., 2008, 2010; Donaire and Lopez-Martinez, 2009; Grellet-Tinner et al., 2012). High G_{H_2O} estimates in some extinct taxa have been used to suggest that their eggs were covered with nest material (e.g., Seymour, 1979; Antunes et al., 1998; Deeming, 2006; Jackson et al., 2008; Grellet-Tinner et al., 2012), because higher values are found in living archosaurs that cover their eggs with nest substrate (i.e., megapodes and crocodiles: e.g., Packard et al., 1979; Seymour and Ackerman, 1980; Deeming and Thompson, 1991).

Estimates of G_{H_2O} values are widely used to predict nesting modes in extinct archosaurs (Seymour, 1979; Williams et al., 1984; Sabath, 1991; Mou, 1992; Grigorescu et al., 1994; Mikhailov et al., 1994; Sahni et al., 1994; Antunes et al., 1998; Deeming, 2006; Jackson et al., 2008, 2010; Donaire and Lopez-Martinez, 2009; Grellet-Tinner et al., 2012). To do so, all previous studies have made two major assumptions for species of living archosaurs, assumptions that have never been statistically tested: 1) covered nests have a higher nest humidity than the other nest types, and thus 2) G_{H_2O} values are higher in species with covered nests than in the species with non-covered nests. In this thesis, nest architecture, nest humidity, and egg water vapor conductance of numerous living archosaur species will be used to statistically test 1) if nest humidity is significantly different among nest types (Chapters Two and Three) and 2) if there is a relationship between nest types and G_{H_2O} (Chapter Four). The ultimate goal of this study is to determine if relationships exist between nest types and water loss of the eggs among living archosaurs that potentially could be used to predict nest types/modes of extinct archosaurs.

CHAPTER TWO: NEST TYPE AND ABSOLUTE HUMIDITY OF LIVING

ARCHOSAUR NESTS

2.1 Introduction

Nest humidity is important during incubation among archosaurs because it affects the rate of water loss from eggs, which is critical for hatching success (Walsberg, 1980; Ar, 1991; Ar and Sidis, 2002). Absolute nest humidity, also known as the water vapor pressure of the nest or P_{nest} (measured in Torr), varies greatly among living archosaur species (Walsberg, 1980; Rahn, 1984; Rahn and Paganelli, 1990; Deeming, 2011), with reported values ranging from 11.00 (*Struthio camelus*: Swart et al., 1987) to 47.80 Torr (*Alectura lathami*: Seymour and Rahn, 1978). This variation in P_{nest} is likely due to the fact that archosaurs build a variety of nest architectures in a variety of habitats and use a variety of incubation behaviors (Coombs, 1989; Rahn and Paganelli, 1990; Rahn, 1991; Hansell, 2000; Ar and Sidis, 2002; Deeming, 2011).

Absolute nest humidity is affected by ambient humidity in which the nest is built (P_a , Torr), as well as by incubation method or behaviors. The absolute ambient humidity of the habitat appears to have a fundamental affect on P_{nest} in that P_{nest} is always equal to or higher than P_a (Staton and Dixon, 1977; Walsberg, 1980; Rahn, 1984, 1991; Waitkuwait, 1985; Rahn and Paganelli, 1990; Deeming, 2011; Charruau, 2012), so P_a represents the minimum value for P_{nest} . Although incubation behaviors may have an effect on nest humidity, archosaurs generally do not appear to actively control the nest humidity through behaviors (Walsberg, 1983; Rahn, 1984; Andersen and Steen, 1986; Ar, 1991; Kern and Cowie, 2000). Absolute nest humidity can be elevated above P_a by incubation of open nests via brooding (Rahn and Paganelli, 1990; Ar and Sidis, 2002) and by incubation of eggs within covered nests (Joanen, 1969; Staton and Dixon, 1977; Waitkuwait, 1985; Booth and Thompson, 1991; Charruau, 2012).

Absolute nest humidity also appears to potentially be affected by the shape or architecture of the nesting materials (Wagner and Seymour, 2001; Deeming, 2011). Scrape nests are shallow depressions on the ground with little or no nest material, and their P_{nest} is shown to be positively correlated with P_a (Deeming, 2011), indicating that P_{nest} increases

with increasing P_a . In scrape nests, P_{nest} is shown to be on average 5 Torr higher than P_a , elevated above P_a via brooding (Deeming, 2011). The P_{nest} of cup-shaped nests of birds tends to be higher than scrape nests at a low P_a because the presence of a nest wall is suggested to insulate the eggs, thus retaining humidity (Deeming, 2011). Also, eggs that are incubated in nests that are completely covered with nesting material during incubation have a high P_{nest} (Joanen, 1969; Staton and Dixon, 1977; Waitkuwait, 1985; Seymour et al., 1987; Booth and Thompson, 1991; Charruau, 2012). These previous studies suggest that the architecture of the nest materials can affect P_{nest} and the amount P_{nest} is raised above P_a . The purpose of this chapter is to determine the relationships among P_{nest} , P_a , and generalized nest types.

2.2 Materials and Methods

Only archosaur species for which measured nest humidity values were available in the literature were used for this study. Nest type and ambient humidity of the nesting habitat for each species were also gleaned from the literature if available.

2.2.1 Nest Humidity

The nest humidity values used for this study include 54 species of birds (spelling of species names follows Clements, 2007) and crocodilians. These nest humidity values, reported as absolute ($= P_{\text{nest}}$) or relative humidity (%) (affected by temperature), have been measured primarily from naturally incubated nests in the field with various hygrometric instruments. In most cases, nest humidity was obtained by the egg hygrometer method (Rahn et al., 1977a), which calculates P_{nest} based on a daily water gain of silica gel inside of the empty eggshell in a nest, using both nest temperature (T_{nest} , °C) and an egg water vapor conductance ($G_{\text{H}_2\text{O}}$, mgH₂O/day/Torr) value. For consistency of this dataset, only values obtained from measurements taken immediately around eggs and underneath a brooding adult in the nest were used. Nest humidity measured in the space around the nest (e.g., Bartholomew et al., 1976; Withers, 1977; White et al., 1978; Simons, 1983; Fitzherbert, 1985; Rahn and Huntington, 1988; Brown, 1994) was excluded because there is a large gradient of nest humidity within a nest (Lill and Fell, 2007). In covered nests of megapodes

and crocodilians, nest humidity was measured from the egg chamber of the nests (Joanen, 1969; Staton and Dixon, 1977; Waitkuwait, 1985; Charruau, 2012), or was determined by previous authors from water content of nest materials (Seymour et al., 1987).

Absolute nest humidity (P_{nest}) values were used for all species. Nest humidity values provided as relative humidity were converted to absolute nest humidity values. For some species, absolute humidity values were taken from Rahn et al. (1977a), who already converted relative humidity into absolute humidity using data from Lomholt (1976). For other species where values were measured in relative humidity (Mayhew, 1955; Joanen, 1969; Staton and Dixon, 1977; Bertram and Burger, 1981; Ponomareva, 1981; Waitkuwait, 1985; Seymour et al., 1987 for *Alectura lathami*; Charruau, 2012), the P_{nest} (absolute nest humidity, Torr) was calculated here from relative humidity (%) and nest temperatures ($^{\circ}\text{C}$), using the equation:

$$P_{\text{nest}} = (\text{relative humidity of nest}) \times 4.583 \times 10^{-2+7.5 \cdot \frac{T_{\text{nest}}}{T_{\text{nest}}+237.3}}. \quad (\text{Eq. 2.1})$$

Calculation of saturated water vapor pressure is based on Tetens (1930). An average absolute nest humidity value was calculated for species that had multiple nest humidity measurements available (i.e., *Anas platyrhynchos*, *Branta leucopsis*, *Charadrius vociferus*, *Larus heermanni*, *Somateria mollissima*, *Struthio camelus*). The non-standard measurement Torr (\equiv mmHg) is used here for absolute nest humidity because it has been used widely in the literature on nest humidity (e.g., Rahn et al., 1977a, 1983; Seymour and Rahn, 1978; Howell, 1979; Rahn and Dawson, 1979; Walsberg, 1980, 1985; Pettit et al., 1981; Ponomareva, 1981; Grant, 1982; Grant et al., 1982a, 1982b, 1984; Whittow et al., 1982, 1989; French and Board, 1983; Vleck et al., 1983; Howey et al., 1984; Rahn, 1984; Andersen and Steen, 1986; Seymour et al., 1987; Swart et al., 1987; Buttemer et al., 1988; Swart and Rahn, 1988; Kern et al., 1990; Rahn and Paganelli, 1990; Booth and Sotherland, 1991), even recently (Deeming, 2011).

2.2.2 Ambient Humidity of Nesting Site

Absolute ambient humidity of the nesting habitats (P_a) of the sampling areas was

obtained for as many species as possible ($n = 40$). For most species, P_a had been measured simultaneously with P_{nest} . Some sampling areas were reported as relative humidity (Mayhew, 1955; Joanen, 1969; Lomholt, 1976; Staton and Dixon, 1977; Bertram and Burger, 1981; Booth, 1985; Waitkuwait, 1985; Lill and Fell, 2007; Charruau, 2012), so here these were converted to absolute values, using mean ambient relative humidity and temperature (T_a , °C) with the Eq. 2.1. Absolute ambient humidity of all megapode and crocodilian species in this chapter was converted. Average ambient relative humidity for megapodes (*Alectura lathami* and *Leipoa ocellata*) was taken from the hatching seasons (September to February for *A. lathami* and November to March for *L. ocellata*) (Booth, 1985). Although Joanen (1969) reported a mean ambient temperature of the nesting site of *Alligator mississippiensis* as 30.7 °C, this value is questionable because his subsequent paper (Joanen and McNease, 1989) shows a much lower T_a (~20 °C). Thus, 20 °C was used for an estimation of P_a for *A. mississippiensis*.

2.2.3 Nest Type

A generalized nest type was assigned for each of the 54 species based on information of nest shape [i.e., scrape, bed, plate, cup, dome, and mound, based on Hansell's (2000) classification] available in the literature.

2.2.4 Statistical Analysis

Absolute nest humidity, ambient humidity, and the gradient between P_{nest} and P_a ($P_{\text{nest}} - P_a$, or ΔP) were compared among different generalized nest types by either one-way analysis of variance (ANOVA) or Kruskal-Wallis tests. One-way ANOVA was applied when the dataset can be assumed parametric and show the equality of variances; otherwise, Kruskal-Wallis test was used. Parametricity of the datasets was checked by Shapiro-Wilk test, which examines non-normal distribution of groups, and the equality of variances of the datasets was analyzed with Levene tests. Tukey's method was chosen for post-hoc multiple comparisons of one-way ANOVA, and pairwise multiple comparisons, which are a default test in the statistical package (see below) using adjusted p values, were also used after Kruskal-Wallis tests. Statistical tests were conducted by IBM SPSS Statistics v. 19.0.0

(SPSS, Inc.).

2.3 Results

2.3.1 Nest Type

Nests of the species were classified into three generalized types based on architecture of nest materials; 1) non-covered scrape nests are those that have little or no vegetation surrounding the eggs; 2) non-covered cup nests are those in which the eggs are not covered with vegetation or sediment, but have vegetation/sediment surrounding the eggs (e.g., bed, plate, cup, dome, and dome and tube nests); and 3) covered nests are those in which the eggs are covered with vegetation and/or sediment (e.g., mound and infilled hole nests) (Table 2.1).

2.3.2 Relationships between P_{nest} and Nest Type

Absolute nest humidity (P_{nest}) ranges from 13.32 to 35.92 Torr, and the mean P_{nest} of all species is 21.96 Torr (Table 2.2; Fig. 2.1). Non-covered nests have P_{nest} values that range from low to relatively high (13.32 to 32.89 Torr; mean 20.70 Torr), with scrape nests ranging from 13.32 to 25.30 Torr and cup nests from 14.00 to 32.89 Torr. Covered nests are generally high and range from 28.41 to 35.92 Torr (mean 32.05 Torr) (Fig. 2.1). Shapiro-Wilk tests and Levene test revealed that each group did not have a distribution that differed significantly from normality (in all cases $p > 0.05$) and the equality of variances was assumed ($p = 0.312$) (Table 2.3); thus, a parametric ANOVA was appropriate. An ANOVA revealed that there was a significant difference in P_{nest} among some of the three nest types (i.e., scrape, cup, and covered nests) ($F_{2, 51} = 16.987$, $p < 0.001$) (Table 2.4). Post-hoc comparisons revealed a significant difference in P_{nest} between covered and non-covered (both scrape and cup) nests (in both cases $p < 0.01$), but no significant difference between scrape and cup nest types ($p = 0.858$) (Table 2.4; Fig. 2.1).

2.3.3 Relationships among Nest Type, P_{nest} and P_a

For each species, P_a is always lower than the P_{nest} (Fig. 2.2). The average P_a for 40 species is 13.98 Torr (range = 3.80 to 24.60 Torr), which is approximately 8 Torr lower than the mean P_{nest} (21.96 Torr) for of all species. For scrape nests, the P_{nest} is on average 4 Torr above the P_a (Fig. 2.3). For cup nests, the P_{nest} is on average 8 Torr higher than P_a . For covered nests, the P_{nest} is on average 16 Torr higher than P_a . Kruskal-Wallis test was used for the gradients between P_{nest} and P_a ($= \Delta P$) due to the violation of parametricity and the equality of variances ($p < 0.05$ for both Shapiro-Wilk tests and Levene test), and it was revealed that a significant difference of ΔP values among three nest types (d.f. = 2, chi-square = 8.835, $p = 0.012$). Pairwise multiple comparisons showed that ΔP is significantly higher in covered nests than non-covered nests (both scrape and cup nests; $p \leq 0.05$), but there is no significant difference between scrape and cup nests ($p = 0.617$: Table 2.4; Fig. 2.3). Also, parametricity and the equality of variances were assumed for the dataset of P_a ($p > 0.05$ for both Shapiro-Wilk tests and Levene test), and an ANOVA showed no significant difference in P_a among the three nest types ($F_{2, 37} = 1.732$, $p = 0.191$) (Table 2.4; Fig. 2.4).

2.4 Discussion

Absolute nest humidity varies greatly among archosaur species due to a variety of factors (e.g., ambient humidity, nesting and brooding behaviors) (Rahn and Paganelli, 1990; Ar and Sidis, 2002; Deeming, 2011). These results also suggest that P_{nest} is also affected by the architecture of the nesting materials. Covered-type nests have a significantly higher P_{nest} than the non-covered nests, including scrape and cup nest types, indicating that covered nests retain more humidity than non-covered nests. Covered nests and high P_{nest} values are found in all megapode birds and crocodilian species in this study.

All megapodes build what are considered here covered nests, where some build large mounds of nesting materials in which the eggs are completely covered and incubated (Table 2.1; Booth and Jones, 2002). These birds tend to have a much higher P_{nest} than non-covered nests of brooding birds, but have a comparable P_{nest} to those of mound-nesting crocodilian species (Table 2.2). Of all archosaur species studied, the megapode *Alectura lathamii* has the highest P_{nest} (35.92, Torr) (Table 2.2), and this value (used here) is a minimum estimate, which was calculated previously using a relative nest humidity of 90 % and a nest

temperature at 34 °C (Seymour et al., 1987). Much higher values have also been predicted, for *A. lathami*, including 47.80 Torr (using the assumption that the mound is saturated at 37.3 °C: Seymour and Rahn 1987), and 35.00 to 45.00 Torr (method not explained: Booth and Thompson, 1991) (Fig. 2.1). *Lepoia ocellata* is the only species of megapode to breed mainly outside tropical regions and in semi-arid areas (del Hoyo et al., 1994; Jones et al., 1995), and it also has a high P_{nest} value (30.70 Torr) (Table 2.2). Additionally, the P_{nest} value used here for *L. ocellata* likely represents a minimum because as it was measured during mid to late incubation period, when relative humidity of the mound has dropped to 77 % (Seymour et al., 1987). In the early incubation period, relative nest humidity is much higher (> 90 %), and thus P_{nest} would be higher than 30.70 Torr (Seymour et al., 1987). Booth and Thompson (1991) also estimated high P_{nest} values of 28.00 to 36.00 Torr for *L. ocellata* (Fig. 2.1), although their method of calculation is not described.

Like megapodes, crocodilian nests are classified here as covered nests, and all crocodilian species build covered hole nests or mound nests. P_{nest} values have been measured for three mound- and one hole-nesting crocodilian species, and are comparable to those of megapodes (Table 2.2). Although relative humidity of many crocodilian nests is close to saturation (Ferguson, 1985), maximum P_{nest} is slightly lower than that of megapodes, likely due to a lower nest temperature (around 30 °C: Table 3 of Ferguson, 1985, as opposed to 33 °C for megapodes: Booth and Jones, 2002). Average P_{nest} of crocodilians is 31.42 Torr, which is close to the absolute humidity of saturated air at 30 °C of 31.83 Torr.

High nest humidity of megapodes and crocodilians can likely be explained by fact that they have covered nests, which help retain humidity. Decaying plant materials and soils of mound nests contain abundant water, ranging from 1.60 to 79.00 % (= $100 \times \text{water mass in nest} / \text{mass of wet nest material}$) (Table 2.5). High water content and warm incubation temperature in mounds (usually > 30 °C for megapodes and > 28 °C for crocodilians: Ferguson, 1985; Booth and Jones, 2002) also contribute to high nest humidity (Waitkuwait, 1985; Seymour et al., 1987). For example, P_{nest} of *L. ocellata* reaches 30.70 Torr when water content at egg level of a mound is 1.67 % on average (Seymour et al., 1987). An egg cavity of a *Crocodylus cataphractus* mound was constantly saturated (= 100 % relative humidity) and the water content of the nest material was 37.00 % (Waitkuwait, 1985).

Therefore, it is likely that the megapode, *Macrocephalon maleo*, and the crocodilians, *Crocodylus acutus*, *C. johnstoni* and *C. palustris*, which also have high water content in their mounds (Whitaker, 1979; Webb et al., 1983; Lutz and Dunbar-Cooper, 1984; Dekker, 1988; Singh and Sager, 1991), also have high P_{nest} values, although P_{nest} values are currently unreported for these species (Table 2.5).

Struthio camelus (ostrich) shows the lowest P_{nest} value (mean 13.32 Torr) of the archosaur species studied (Table 2.2). The ostrich builds a scrape nest on the ground without any nest materials in arid environments, such as savanna, steppe, or desert grasslands, including true desert (Namib Desert) (Goodfellow, 1977; Serle and Morel, 1977; del Hoyo et al., 1992; Davies, 2002; Dean, 2004). Because P_{nest} of scrape nests is correlated with (Deeming, 2011) and parallels (Swart et al., 1987) ambient humidity of the nesting habitat, the low P_{nest} value of *S. camelus* is likely due to a combination of the nest type (no insulating nest materials) and low ambient humidity (mean 9.74 Torr) of the nesting habitat. Further data is required, however, to test if scrape nests in arid environments show significantly lower P_{nest} than other nest types in these environments.

Egg incubation, whether it occurs within covered nests or via brooding in non-covered nests, results in a P_{nest} that is almost always elevated above P_a (Table 2.2; Fig. 2.2). Ambient humidity has a fundamental affect on P_{nest} in that it represents the minimum value for P_{nest} . Therefore, it was tested here if certain nest architectures had a higher P_{nest} relative to their P_a , essentially eliminating the effects of P_a . There appears to be a general trend in the effect of nest architecture on P_{nest} relative to P_a : scrape nests, on average, with no or little nest materials have a P_{nest} slightly above ambient humidity (4 Torr); nests with nesting material around but not covering the eggs (i.e., cup nests) have P_{nest} that is higher above the P_a than for scrape nests (8 Torr); and nests where the eggs are completely covered by nesting material have P_{nest} that is even higher above ambient humidity than for cup nests (16 Torr). Covered nests have a significantly higher increase in P_{nest} relative to P_a than scrape or cup nests, although there were no significant differences between these parameters between scrape and cup nests. The results here suggest that the architecture of the nesting material surrounding the eggs has an effect on P_{nest} in that P_{nest} increases more above P_a with increasing enclosure of the eggs with nest materials.

Table 2.1: Three generalized nest types established in this study, based on nest architecture


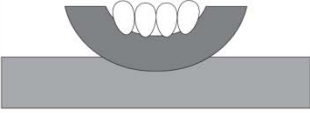
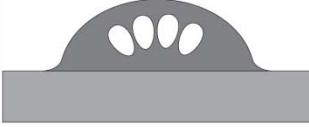
Nest type	Non-covered scrape nest	Non-covered cup nest	Covered nest
			
Description	Shallow depressions on the ground with little or no nest material	Bed, plate, cup, or dome-shaped nest on and above the ground with nest materials of plant and sediment	Mound (heap of moisture soil and/or plant materials) or infilled hole nest on/in the ground
Egg nature	No nest material covers eggs	Eggs are partially covered with nest material	Eggs are completely covered with nest material
Example	<i>Struthio camelus</i> , <i>Gelochelidon nilotica</i>	<i>Cygnus olor</i> , <i>Ficedula hypoleuca</i>	<i>Alectura lathamii</i> , <i>Alligator mississippiensis</i>

Table 2.2: Nest types and humidity variables relevant to nesting for archosaur species

Data used for statistical analyses in Chapter Two. Field measurements of mean absolute nest humidity (P_{nest}), absolute ambient humidity of the environment in which the nest was built (P_a), gradient between P_{nest} and P_a (ΔP) were averaged if multiple values were available for a species. Note that *Gygis alba* was assigned to scrape nest due to the lack of nest materials as classified by Deeming (2011), although eggs are laid on bare tree branches.

<i>Species</i>	P_{nest} (Torr)	P_a (Torr)	ΔP (Torr)	Nest type	Sources
Anseriformes					
<i>Alopochen aegyptiaca</i>	19.20	18.10	1.10	Cup	Rahn et al. (1977a); del Hoyo et al. (1992)
<i>Anas platyrhynchos</i>	19.85	14.21	5.64	Cup	Mayhew (1955); Rahn et al. (1977a); French and Board (1983); del Hoyo et al. (1992); Kear (2005)
<i>Anser anser</i>	22.30	21.00	1.30	Cup	Harrison (1975); Rahn et al. (1977a); del Hoyo et al. (1992)
<i>Aythya novaeseelandiae</i>	15.30			Cup	Oliver (1955); French and Board (1983); Kear (2005)
<i>Branta leucopsis</i>	17.40	6.76	10.64	Cup	Harrison (1975); Rahn et al. (1983); Howey et al. (1984); del Hoyo et al. (1992); Kear (2005)
<i>Cereopsis novaehollandiae</i>	23.83			Cup	Pizzey (1980); Wagner and Seymour (2001)
<i>Chen caerulescens</i>	24.20	22.80	1.40	Cup	Rahn et al. (1977a); del Hoyo et al. (1992)
<i>Clangula hyemalis</i>	14.90	3.80	11.10	Cup	Harrison (1975); Rahn et al. (1983); del Hoyo et al. (1992)

<i>Cygnus atratus</i>	22.42	11.35	11.07	Cup	Howey et al. (1984); del Hoyo et al. (1992); Kear (2005)
<i>Cygnus cygnus</i>	32.89			Cup	Howey et al. (1984); del Hoyo et al. (1992); Kear (2005)
<i>Cygnus olor</i>	25.90			Cup	Booth and Sotherland (1991); del Hoyo et al. (1992)
<i>Oxyura leucocephala</i>	21.50			Cup	Harrison (1975); French and Board (1983); del Hoyo et al. (1992)
<i>Oxyura vittata</i>	26.00			Cup	French and Board (1983); del Hoyo et al. (1992); Kear (2005)
<i>Somateria mollissima</i>	21.60	6.09	15.51	Cup	Harrison (1975); Lomholt (1976); French and Board (1983); Rahn et al. (1983); del Hoyo et al. (1992)
Charadriiformes					
<i>Charadrius vociferous</i>	21.75	15.20	6.55	Scrape	Rahn et al. (1977a); Grant (1982); del Hoyo et al. (1996); Baicich and Harrison (1997)
<i>Gelochelidon nilotica</i>	20.50	20.20	0.30	Scrape	Grant et al. (1984); del Hoyo et al. (1996); Baicich and Harrison (1997)
<i>Gygis alba</i>	14.60			Scrape	Pettit et al. (1981); del Hoyo et al. (1996); Niethammer and Patrich-Castilaw (1998); Vanderwerf (2003)
<i>Himantopus mexicanus</i>	16.90	16.15	0.75	Scrape	Grant (1982); del Hoyo et al. (1996); Baicich and Harrison (1997)
<i>Larus heermanni</i>	18.49	17.30	1.19	Cup	Rahn et al. (1977a); Rahn and Dawson (1979); del Hoyo et al. (1996); Baicich and Harrison (1997)

<i>Larus livens</i>	26.10	24.60	1.50	Cup	Rahn et al. (1977a); del Hoyo et al. (1996); Baicich and Harrison (1997)
<i>Pluvianus aegyptius</i>	22.85			Scrape	Howell (1979); del Hoyo et al. (1996)
<i>Recurvirostra americana</i>	24.20	16.90	7.30	Scrape	Grant (1982); del Hoyo et al. (1996); Baicich and Harrison (1997)
<i>Rynchops niger</i>	25.30	20.20	5.10	Scrape	Grant et al. (1984); del Hoyo et al. (1996); Baicich and Harrison (1997)
<i>Sterna forsteri</i>	20.40	15.20	5.20	Scrape	Rockwell (1911); Godfrey (1966); Grant (1982); Semenchuk (1993); del Hoyo et al. (1996); Baicich and Harrison (1997)
Ciconiiformes					
<i>Ardea albus</i>	15.00	12.00	3.00	Cup	Vleck et al. (1983); del Hoyo et al. (1992); Baicich and Harrison (1997)
<i>Eudocimus albus</i>	14.00	11.00	3.00	Cup	Vleck et al. (1983); del Hoyo et al. (1992); Baicich and Harrison (1997)
Columbiformes					
<i>Columba livia</i>	19.00	10.07	8.93	Cup	Harrison (1975); Lomholt (1976); del Hoyo et al. (1997)
<i>Streptopelia senegalensis</i>	20.27			Cup	Harrison (1975); Ponomareva (1981)
<i>Zenaida macroura</i>	18.20	11.10	7.10	Cup	Walsberg (1985); Baicich and Harrison (1997); del Hoyo et al. (1997)
Coraciiformes					

<i>Merops ornatus</i>	26.18	12.14	14.04	Cup	del Hoyo et al. (2001); Lill and Fell (2007)
Galliformes					
<i>Alectura lathamii</i>	35.92	8.35	27.57	Covered	Seymour and Rahn (1978); Booth (1985); Seymour et al. (1987); Pizzey (1980)
<i>Gallus gallus</i>	15.00			Cup	Lomholt (1976); Pizzey (1980); del Hoyo et al. (1994)
<i>Lagopus lagopus</i>	21.10	5.20	15.90	Cup	Andersen and Steen (1986); del Hoyo et al. (1994)
<i>Leipoa ocellata</i>	30.70	7.97	22.73	Covered	Pizzey (1980); Booth (1985); Seymour et al. (1987); del Hoyo et al. (1994)
<i>Phasianus colchicus</i>	20.00	18.80	1.20	Cup	Harrison (1975); Rahn et al. (1977a); del Hoyo et al. (1994)
Gruiformes					
<i>Gallinula tenebrosa</i>	27.00	8.19	18.81	Cup	Lill (1990); del Hoyo et al. (1996)
<i>Porphyrio porphyrio</i>	27.75	8.19	19.56	Cup	Lill (1990); del Hoyo et al. (1996)
Passeriformes					
<i>Cercotrichas galactotes</i>	15.53			Cup	Harrison (1975); Ponomareva (1981)
<i>Ficedula hypoleuca</i>	15.75	12.00	3.75	Cup	Harrison (1975); Kern and Cowie (1995); del Hoyo et al. (2006)
<i>Melospiza melodia micronyx</i>	16.10	8.10	8.00	Cup	Kern et al. (1990); del Hoyo et al. (2009)
<i>Parus major</i>	18.00			Cup	Harrison (1975); Lomholt (1976); del Hoyo et al. (2007)
<i>Passer ammodendri</i>	25.54			Cup	Ponomareva (1981); del Hoyo et al. (1992)

<i>Scotocerca inquieta</i>	30.29			Cup	Harrison (1975); Ponomareva (1981)
Pelecaniformes					
<i>Sula sula</i>	26.96	15.90	11.06	Cup	Pizzey (1980); Whittow et al. (1989); del Hoyo et al. (1992)
Procellariiformes					
<i>Phoebastria immutabilis</i>	19.10	13.70	5.40	Cup	Dill (1916); Grant et al. (1982b); del Hoyo et al. (1992)
<i>Phoebastria nigripes</i>	17.30	13.70	3.60	Cup	Richards (1909); Grant et al. (1982b); del Hoyo et al. (1992); Whittow (1993)
<i>Pterodroma hypoleuca</i>	18.10	14.90	3.20	Cup	Howell and Bartholomew (1961); Grant et al. (1982a); del Hoyo et al. (1992)
<i>Puffinus pacificus</i>	19.57	17.25	2.32	Cup	Howell and Bartholomew (1961); Whittow et al. (1982); del Hoyo et al. (1992); Whittow (1997)
Struthioniformes					
<i>Dromaius novaehollandiae</i>	16.05	9.25	6.80	Cup	Pizzey (1980); Buttemer et al. (1988); del Hoyo et al. (1992)
<i>Struthio camelus</i>	13.32	9.74	3.58	Scrape	Goodfellow (1977); Serle and Morel (1977); Bertram and Burger (1981); Swart et al. (1987); Swart and Rahn (1988); del Hoyo et al. (1992)
Crocodylia					
<i>Alligator mississippiensis</i>	29.95			Covered	Joanen (1969); Coombs (1989); Joanen and McNease (1989)

<i>Caiman crocodiles</i>	28.41	22.10	6.31	Covered	Staton and Dixon (1977); Brazaitis and Watanabe (2011)
<i>Crocodylus acutus</i>	34.19	24.36	9.83	Covered	Brazaitis and Watanabe (2011); Charruau (2012)
<i>Crocodylus cataphractus</i>	33.14	21.42	11.72	Covered	Waitkuwait (1985); Brazaitis and Watanabe (2011)

Table 2.3: Results of (A) Shapiro-Wilk tests and (B) Levene tests for P_{nest} , P_a , and ΔP . The results indicate there are no significant differences for P_{nest} and P_a (in all cases $p > 0.05$), which allows using one-way ANOVA, while p values are lower than 0.05 for ΔP , which indicates Kruskal-Wallis test is more appropriate in this case.

(A)

Variable	Nest type	n	W value	p
P_{nest}	Uncovered scrape nest	9	0.935	0.534
	Uncovered cup nest	39	0.945	0.057
	Covered nests	6	0.966	0.866
P_a	Uncovered scrape nest	7	0.898	0.319
	Uncovered cup nest	27	0.976	0.772
	Covered nests	6	0.861	0.192
ΔP	Uncovered scrape nest	7	0.908	0.381
	Uncovered cup nest	27	0.892	0.009
	Covered nests	6	0.951	0.747

(B)

Test	d.f.	F value	p
P_{nest} : scrape vs. cup vs. covered nests	2, 51	1.192	0.312
P_a : scrape vs. cup vs. covered nests	2, 37	2.879	0.069
ΔP : scrape vs. cup vs. covered nests	2, 37	3.509	0.040

Table 2.4: Results of (A) one-way ANOVAs and (B) Kruskal-Wallis test with post-hoc comparisons of P_{nest} , P_a , and ΔP among three nest types

The results indicate covered nests have significantly higher P_{nest} and ΔP than the other nest types (in all cases $p \leq 0.05$), but there is no significance in P_a ($p \gg 0.05$).

(A)

Test	d.f.	F value	p	Tukey test	p
P_{nest} : scrape vs. cup vs. covered nests	2, 51	16.987	2.220×10^{-6}	Scrape vs. Cup	0.858
				Scrape vs. Covered	1.652×10^{-5}
				Cup vs. Covered	2.160×10^{-6}
P_a : scrape vs. cup vs. covered nests	2, 37	1.732	0.191	Scrape vs. Cup	0.320
				Scrape vs. Covered	0.999
				Cup vs. Covered	0.345

(B)

Test	d.f.	χ^2 value	p	Multiple comparison	Adjusted p
ΔP : scrape vs. cup vs. covered nests	2	8.835	0.012	Scrape vs. Cup	0.617
				Scrape vs. Covered	0.011
				Cup vs. Covered	0.050

Table 2.5: Water content and nest humidity for covered nests of archosaur species

Sources: 1, Seymour et al. (1987); 2, Booth and Seymour (1984); 3, Dekker (1988, 1990); 4, Joanen (1969); 5, Chabreck (1975); 6, Lutz and Dunber-Cooper (1984); 7, Waitkuwait (1985); 8, Webb et al. (1983); 9, Whitaker (1979); 10, Singh and Sager (1991).

<i>Species</i>	Water content (%)	P _{nest} (Torr)	Sources
<i>Alectura lathami</i>	13.04 – 33.33 (mean 24.13)	35.92	1
<i>Leipoa ocellata</i>	1.67 – 60.00?	30.70	1, 2
<i>Macrocephalon maleo</i>	1.60 – 45.00 (main range 6.00 – 12.00)	?	3
<i>Alligator mississippiensis</i>	45.40 – 79.00 (mean 71.20)	30.94	4, 5
<i>Crocodylus acutus</i>	4.89 – 36.14	?	6
<i>Crocodylus cataphractus</i>	37.00	32.75	7
<i>Crocodylus johnstoni</i>	2.60 – 5.60	?	8
<i>Crocodylus palustris</i>	5.00 – 15.00	?	9, 10

Figure 2.1: Boxplot of P_{nest} among scrape, cup, and covered nest types in archosaur species. Estimated P_{nest} ranges of covered nests of *Alectura lathamii* and *Leipoa ocellata* are also shown. Note high P_{nest} values of covered nest type. Arrows indicate p values of post-hoc tests after one-way ANOVA.

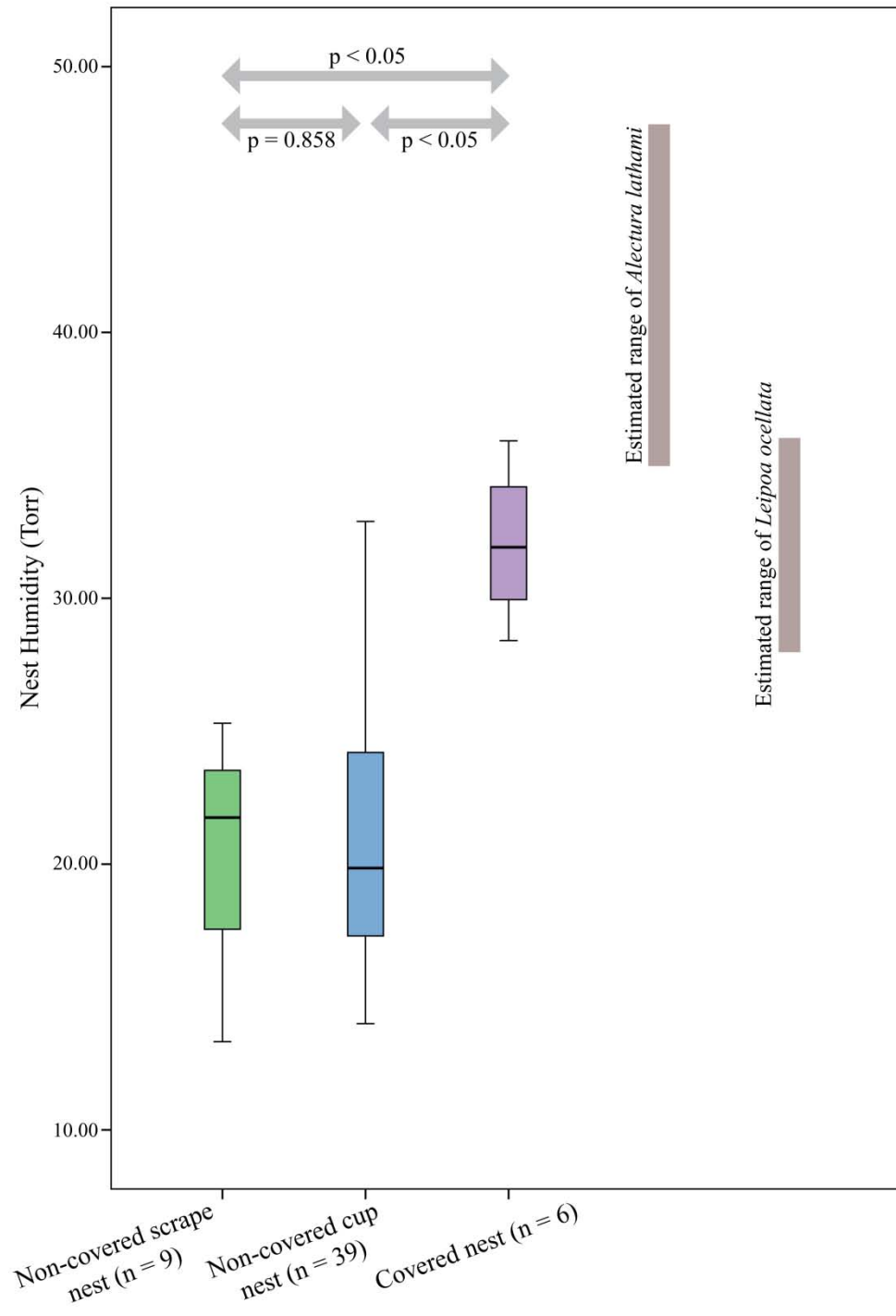


Figure 2.2: Scatter plot of mean P_{nest} and P_a values for 40 archosaur species

Note that P_{nest} is always higher than P_a . The grey line indicates a theoretical minimum limit of P_{nest} , in which P_{nest} is equal to P_a .

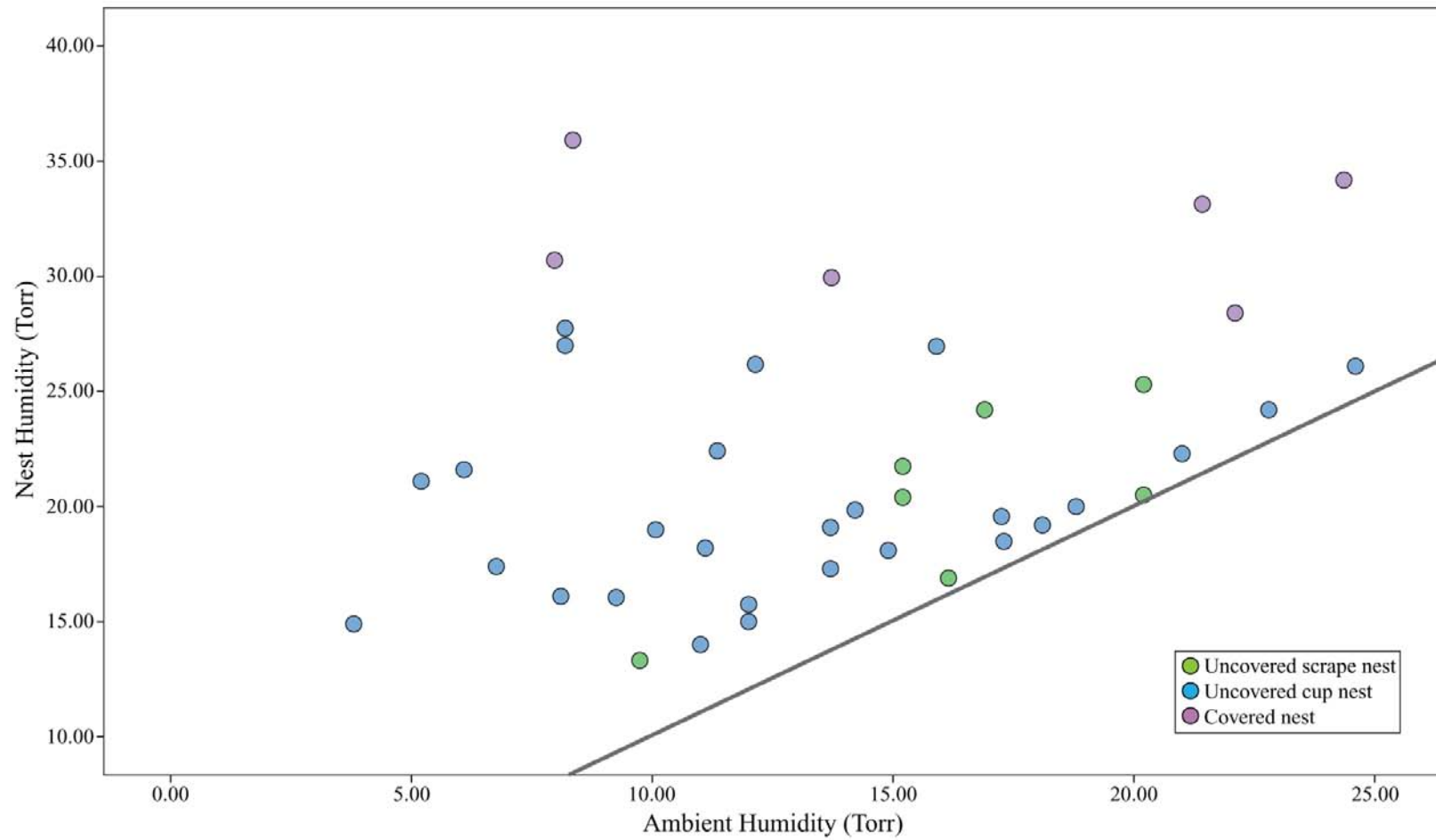


Figure 2.3: Boxplot of $\Delta P (= P_{\text{nest}} - P_a)$ among three nest types

Note high ΔP values of covered nest type. Arrows indicate p values of post-hoc tests after Kruskal-Wallis test.

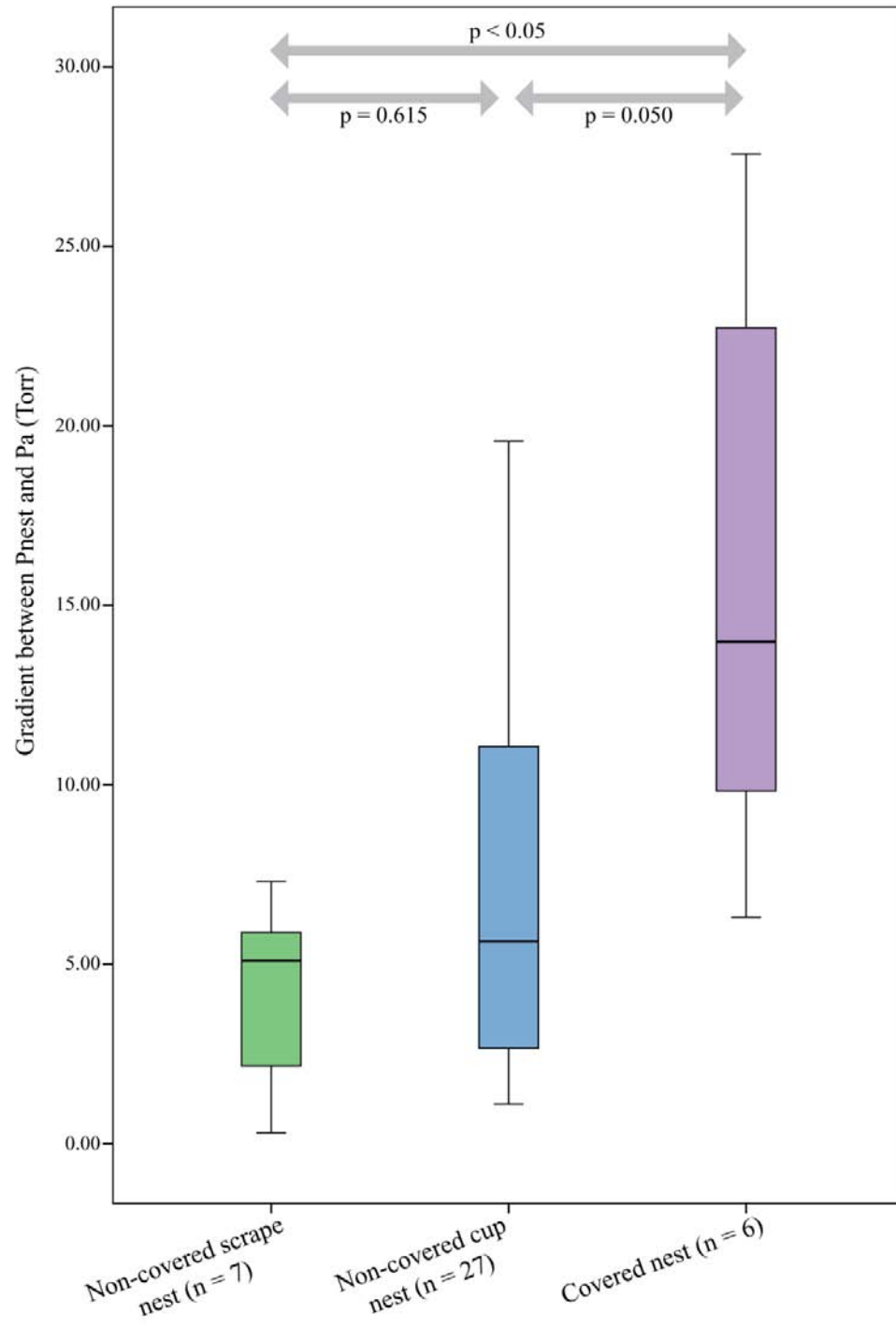
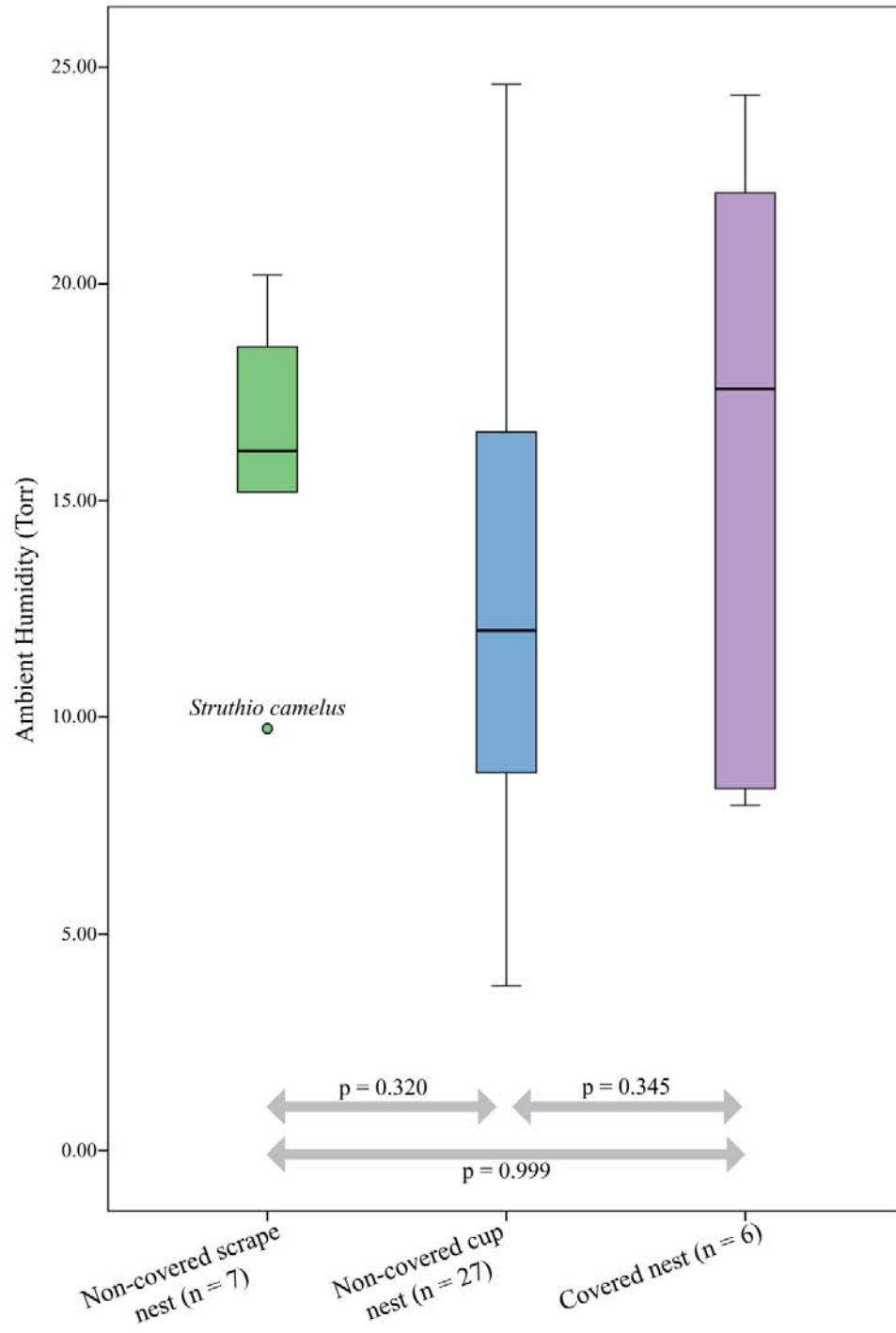


Figure 2.4: Boxplot of P_a among three nest types

Note that there are no significant differences among nest types ($p > 0.05$). Arrows indicate p values of post-hoc tests after one-way ANOVA.



CHAPTER THREE: NEST HUMIDITY OF HIGHLY AQUATIC BIRDS

3.1 Introduction

Grebes (Order Podicipediformes) are unusual in that their nesting is highly adapted to aquatic environments. They build floating beds of wet aquatic vegetation on water (e.g., ponds, lakes, and rivers), with or without anchors (del Hoyo et al., 1992; Fjeldsa, 2004). The nest cup, which contains the eggs, is situated close to water table (just above the water surface) (Bochenski, 1961; Storer, 1992; Storer and Nuechterlein, 1992; Muller and Storer 1999; Stedman, 2000), and the bottom of nest cup is sometimes submerged (Sotherland et al., 1984; Muller and Storer, 1999). Their nests are therefore sodden (e.g., Roberts, 1936; Lomholt, 1976; Goodfellow, 1977; Terres, 1980; Davis et al., 1984; Sotherland et al., 1984; Storer and Nuechterlein, 1992; Muller and Storer, 1999) and even the eggs are likely to be wet (Davis et al., 1984; Sotherland et al., 1984; Cullen et al., 1999; Stedman, 2000). Thus, the nest is assumed to be saturated (Carey, 1980b, 2002; Davis et al., 1984).

Although grebes build non-covered cup nests and brood their eggs like other birds, the adults sometimes cover the eggs with wet vegetation when they leave the nests (e.g., Davis et al., 1984; Storer and Nuechterlein, 1992; Stout and Nuechterlein, 1999; Prokop and Trnka, 2011). The eggs are thus only sometimes covered, unlike nests of megapodes and crocodilians, which are covered throughout incubation and are known to have a high P_{nest} (Chapter Two). It is anticipated here, however, that the extreme aquatic nesting style and the wetness of grebe nests would also result in a high P_{nest} , although P_{nest} has never been measured for grebes or other aquatic birds with wet nests (including loons, jacanas, and black terns: Bent, 1963; Bergman et al., 1970; Goodfellow, 1977; Dunn and Agro, 1995; McIntyre and Barr, 1997; Jenni and Mace, 1999). In this chapter, P_{nest} values are calculated for the wet non-covered nests of such aquatic nesting birds. Among such wet aquatic nesters, only the P_{nest} for grebes and the Black Tern (*Chlidonias niger*) could be estimated as the necessary data is available for only these birds in the literature.

3.2 Materials and Methods

Absolute nest humidity (P_{nest} , Torr) of three grebe species (*Podiceps cristatus*, *P.*

nigricollis, and *Podilymbus podiceps*) and the Black Tern (*Chlidnias niger*) was estimated based on nest temperatures (T_{nest} , °C) available in the literature. Maximum P_{nest} for these species should be equal to saturated water vapor pressure of the nest temperature, because their soaked floating nests are likely saturated (Carey, 1980b, 2002; Davis et al., 1984; Dunn and Agro, 1995). Saturated water vapor pressure (= maximum P_{nest} , Torr) was calculated using Tetens' (1930) formula:

$$\text{Saturated water vapor pressure} = 4.583 \times 10^{7.5 \cdot T / (T + 237.3)} \quad (\text{Eq. 3.1})$$

where T is temperature (°C) (in this case equal to T_{nest}). Mean nest temperature was obtained from the literature, which has been measured at the bottom of the nest cup of wet aquatic nests in the field using thermometers (Schiermann, 1927; Bochenski, 1961; Davis, 1983; Davis et al., 1984), or measured with thermocouples inserted in a fake egg in a natural nest (Sotherland, 1982). Nest temperature of *P. nigricollis* was averaged among the data of Bochenski (1961) and Sotherland (1982). Ambient air temperature of the nesting habitat (T_a , °C) was also obtained from the literature for a comparison with nest temperature.

The three grebe species and the Black Tern were then tested to determine if their calculated P_{nest} values are closer to P_{nest} of covered-type nests (i.e., mounds and infilled holes) or to non-covered nests (cup and scrape nests), using linear discriminate analysis by IBM SPSS Statistics v. 19.0.0 (SPSS, Inc.). Absolute nest humidity, compiled in Table 2.2, was used as an independent variable, which in that chapter revealed a significant difference between covered (six species) and non-covered nests (48 species) (see Chapter Two). Grebes and black terns were classified into either covered nest type or non-covered nest type in this chapter.

3.3 Results

Maximum P_{nest} for four species of aquatic nesters (*Chlidnias niger*, *Podiceps cristatus*, *P. nigricollis*, and *Podilymbus podiceps*) was estimated based on nest temperature, with an assumption that relative nest humidity is saturated (Table 3.1; Fig. 3.1). Nest temperature, directly measured in the field, ranges mainly from 24.97 to 32.00 °C (mean 28.49 °C). The

mean maximum P_{nest} for the four species of aquatic nesters is 30.40 Torr, with a main range of 24.19 to 35.67 Torr. Mean T_a of the nesting habitats (17.78 °C) is much lower than mean T_{nest} (28.49 °C), indicating P_{nest} is much higher than P_a .

The linear discriminate analysis revealed that P_{nest} of *Chlidnias niger*, *Podiceps nigricollis* and *Podilymbus podiceps* is comparable to that of covered-type nests (megapodes and crocodilians), whereas P_{nest} of *Podiceps cristatus* is closer to that of non-covered nest type (Wilk's lambda = 0.603, $p \ll 0.001$: Table 3.2). This analysis showed high accuracy (90.7 %), as among 54 bird and crocodilian species, all megapode and crocodilian species ($n = 6$) were correctly identified as the covered nest type and only five species of 48 non-covered species incorrectly fell into the covered nest type due to relatively high P_{nest} values.

3.4 Discussion

In Chapter Two, it was shown that covered type nests have a significantly higher nest humidity than non-covered nest type in archosaur species for which measured P_{nest} values were available. In this chapter, P_{nest} was estimated for a limited number of highly aquatic nester species (*Chlidnias niger*, *Podiceps cristatus*, *P. nigricollis*, and *Podilymbus podiceps*) because it was anticipated that, although their nests are non-covered, their unusually wet nesting styles could result in high nest humidity. Estimated mean P_{nest} of three species of grebes and the Black Tern (30.40 Torr) is high and is similar to that of covered nests (32.05 Torr) of crocodilians and megapodes, but is considerably higher than mean P_{nest} of the other non-covered nests (20.70 Torr). Davis et al. (1984) also predicted a high P_{nest} value for the grebe, *Podilymbus podiceps* (32.00 Torr), based on daily water loss of egg in the field, water vapor conductance, and saturated P_{egg} . The high P_{nest} in grebes and black terns is likely due to an unusual aquatic nesting style of these birds.

Absolute nest humidity of the aquatic nests of grebes calculated here is probably high due to a combination of wet nest materials and behaviors of brooding adults. In addition to building wet nests on water, brooding grebes cover their nests with soaked plant materials when they leave the nest (e.g., Davis et al., 1984; Storer and Nuechterlein, 1992; Stout and Nuechterlein, 1999; Prokop and Trnka, 2011), which helps regulate nest temperature and humidity, and avoids depredation (Prokop and Trnka, 2011). Like grebes, the aquatic nests

of the Black Tern, *Chlidonias niger* are usually floating on water and the nest is wet (Cuthbert, 1954; Bent, 1963; Bergman et al., 1970; Davis and Ackerman, 1985). The nest cup is assumed to be saturated (Dunn and Agro, 1995), and here the estimated P_{nest} for this taxon is also high. A high P_{nest} likely exists in other aquatic nesters, such as loons and jacanas, which also build wet floating nests (Goodfellow, 1977; McIntyre and Barr, 1997; Jenni and Mace, 1999). Nest humidity of highly aquatic nesters, such as grebes and black terns, therefore indicates that high P_{nest} may not be limited to species with covered-type nests as shown in Chapter Two, but that there could be some species with unusual nesting styles or behaviors that also produce a high nest humidity.

One non-aquatic nester that sometimes is shown to have a high P_{nest} value is *Pluvianus aegyptius* (Egyptian Plover), a bird also known to have a unique nesting style. These birds are scrape nesters (Howell, 1979; Seymour and Ackerman, 1980; Rahn, 1984), and lay their eggs in sandbars of tropical regions during the dry season (Howell, 1979; Maclean, 1996). The eggs are completely or partially covered with sands, probably for concealment and thermoregulation, and the incubating adult sits on the nest (Howell, 1979). The P_{nest} for *P. aegyptius* is low normally (14.50 Torr) (Howell, 1979), but occasionally the adult moistens its belly plumage with water known as “belly-soaking behavior” (Maclean, 1975), to regulate nest temperature on hot days, which increases P_{nest} significantly (31.20 Torr) (Howell, 1979). This suggests other behaviors can also increase P_{nest} of non-covered nests, although in this example, occasionally. This example, however, further serves to highlight that, different nesting styles or behaviors can increase nest humidity of open or non-covered nests.

Covered nests of megapodes and crocodilians, hypothesized to have significantly higher P_{nest} due to the enclosed nest architecture in Chapter Two, are also composed of wet nest materials, which contain a large amount of water (Table 2.5; Joanen, 1969; Chabreck, 1975; Whitaker, 1979; Webb et al., 1983; Booth and Seymour, 1984; Lutz and Dunber-Cooper, 1984; Waitkuwait, 1985; Seymour et al., 1987; Dekker, 1988, 1990) and retain moisture. Their nesting styles are unusual relative to other archosaurs in that the enclosed nests (mound or infilled hole) are built on or in the ground. In megapodes, rainfall contributes to water content of the mounds during the nest-construction period (Fleay, 1937; Frith, 1956), and the moisture level of mounds is maintained by modification of

mound shape by the adults through incubation (Fleay, 1937; Frith, 1962; Seymour et al., 1986, 1987; Jones et al., 1995). In crocodilians, high water content of nests likely result from the proximity of nests to water (e.g., ponds, rivers), abundant rainfall, and adult behaviors (e.g., urination) (e.g., Chabreck, 1975; Whitaker and Whitaker, 1977). High nest humidity in covered nest types thus likely results from a combination of the enclosed nest architecture and the moisture of nesting materials (Waitkuwait, 1985; Seymour et al., 1987).

Table 3.1: Mean values of estimated maximum P_{nest} for wet aquatic nests

Mean temperature of ambient air (T_a) and mean temperature of nests (T_{nest}) also reported, as measured in the field. Sources: 1, Schiermann (1927); 2, Bochenski (1961); 3, Sotherland (1982); 4, Davis et al. (1984); 5, Davis (1983).

<i>Species</i>	T_a (°C)	T_{nest} (°C)	Estimated P_{nest} (Torr)	Sources
<i>Podiceps cristatus</i>	16.96	24.97	24.19	1
<i>Podiceps nigricollis</i>	19.75	25.22	29.49	2, 3
<i>Podilymbus podiceps</i>	17.20	31.75	35.25	4
<i>Chlidnias niger</i>	17.20	32.00	35.67	5
Mean	17.78	28.49	30.40	

Table 3.2: Results of linear discriminate analysis of P_{nest} in 58 archosaur species

The results indicate that P_{nest} of two grebe species (*Podiceps nigricollis* and *Podilymbus podiceps*) and the Black Tern (*Chlidnias niger*) classify as covered nest types, whereas *Podiceps cristatus* classify as non-covered nest type. P_{nest} values of all species, except grebes and black terns, are from Table 2.2. P_{nest} of aquatic nesters calculated based on T_{nest} . Incorrect classifications are bolded, and rows of grebes and the Black Tern highlighted in blue. Probability of nest type prediction in ‘p’ column.

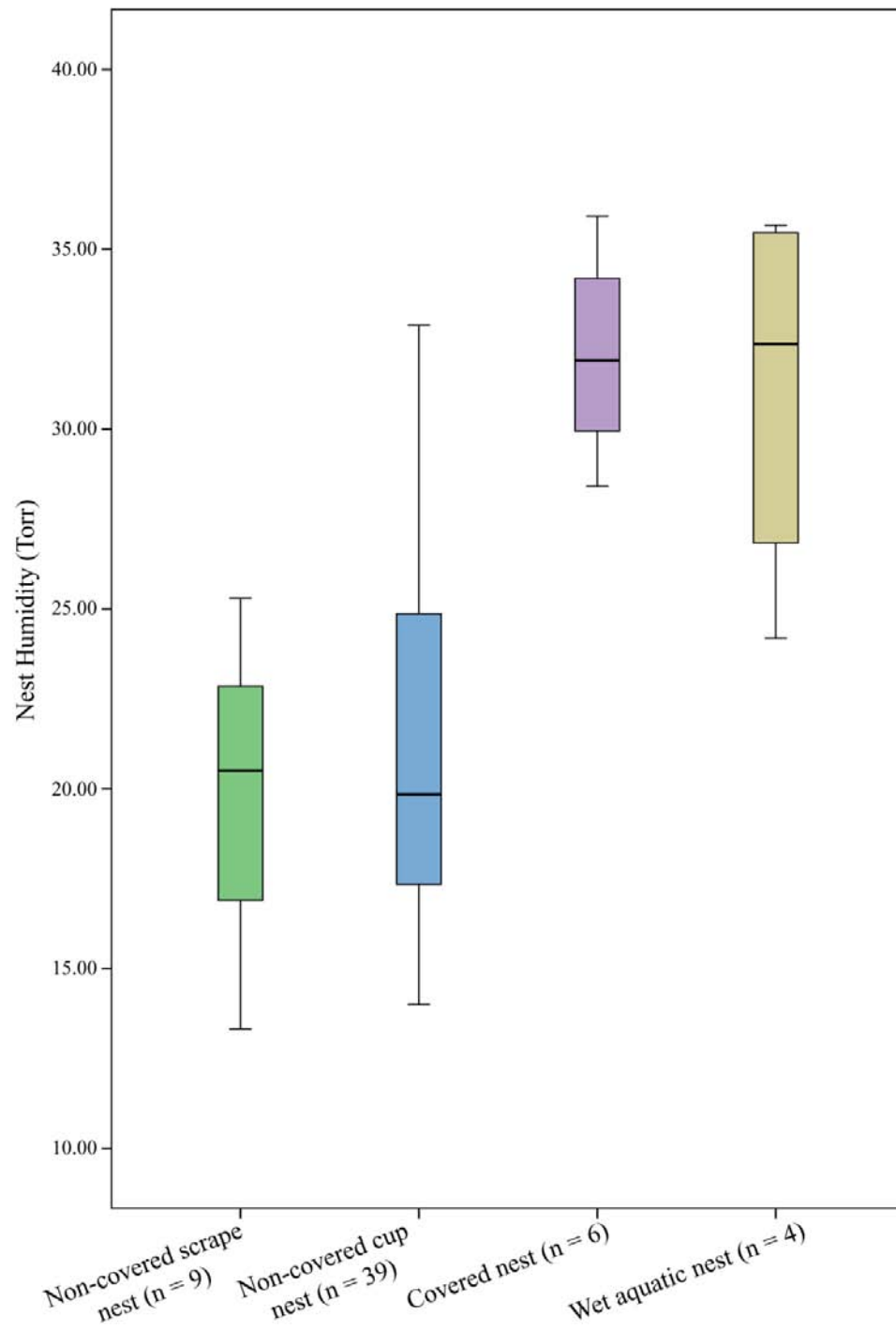
<i>Species</i>	P_{nest} (Torr)	Observed nest type	Predicted nest type	p
<i>Struthio camelus</i>	13.32	Non-covered nest	Non-covered nest	0.999
<i>Eudocimus albus</i>	14.00	Non-covered nest	Non-covered nest	0.999
<i>Gygis alba</i>	14.60	Non-covered nest	Non-covered nest	0.999
<i>Clangula hyemalis</i>	14.90	Non-covered nest	Non-covered nest	0.998
<i>Ardea albus</i>	15.00	Non-covered nest	Non-covered nest	0.998
<i>Gallus gallus</i>	15.00	Non-covered nest	Non-covered nest	0.998
<i>Aythya novaeseelandiae</i>	15.30	Non-covered nest	Non-covered nest	0.998
<i>Cercotrichas galactotes</i>	15.53	Non-covered nest	Non-covered nest	0.998
<i>Ficedula hypoleuca</i>	15.75	Non-covered nest	Non-covered nest	0.998
<i>Dromaius novaehollandiae</i>	16.05	Non-covered nest	Non-covered nest	0.997
<i>Melospiza melodia micronyx</i>	16.10	Non-covered nest	Non-covered nest	0.997
<i>Himantopus mexicanus</i>	16.90	Non-covered nest	Non-covered nest	0.995
<i>Phoebastria nigripes</i>	17.30	Non-covered nest	Non-covered nest	0.994
<i>Branta leucopsis</i>	17.40	Non-covered nest	Non-covered nest	0.994
<i>Parus major</i>	18.00	Non-covered nest	Non-covered nest	0.991
<i>Pterodroma hypoleuca</i>	18.10	Non-covered nest	Non-covered nest	0.991
<i>Zenaida macroura</i>	18.20	Non-covered nest	Non-covered nest	0.990
<i>Larus heermanni</i>	18.49	Non-covered nest	Non-covered nest	0.988
<i>Columba livia</i>	19.00	Non-covered nest	Non-covered nest	0.985
<i>Phoebastria immutabilis</i>	19.10	Non-covered nest	Non-covered nest	0.984

<i>Alopochen aegyptiaca</i>	19.20	Non-covered nest	Non-covered nest	0.983
<i>Puffinus pacificus</i>	19.57	Non-covered nest	Non-covered nest	0.979
<i>Anas platyrhynchos</i>	19.85	Non-covered nest	Non-covered nest	0.975
<i>Phasianus colchicus</i>	20.00	Non-covered nest	Non-covered nest	0.973
<i>Streptopelia senegalensis</i>	20.27	Non-covered nest	Non-covered nest	0.969
<i>Sterna forsteri</i>	20.40	Non-covered nest	Non-covered nest	0.967
<i>Gelochelidon nilotica</i>	20.50	Non-covered nest	Non-covered nest	0.965
<i>Lagopus lagopus</i>	21.10	Non-covered nest	Non-covered nest	0.951
<i>Oxyura leucocephala</i>	21.50	Non-covered nest	Non-covered nest	0.940
<i>Somateria mollissima</i>	21.60	Non-covered nest	Non-covered nest	0.937
<i>Charadrius vociferous</i>	21.75	Non-covered nest	Non-covered nest	0.931
<i>Anser anser</i>	22.30	Non-covered nest	Non-covered nest	0.909
<i>Cygnus atratus</i>	22.42	Non-covered nest	Non-covered nest	0.903
<i>Pluvianus aegyptius</i>	22.85	Non-covered nest	Non-covered nest	0.880
<i>Cereopsis novaehollandiae</i>	23.83	Non-covered nest	Non-covered nest	0.808
<i>Chen caerulescens</i>	24.20	Non-covered nest	Non-covered nest	0.773
<i>Recurvirostra Americana</i>	24.20	Non-covered nest	Non-covered nest	0.773
<i>Rynchops niger</i>	25.30	Non-covered nest	Non-covered nest	0.647
<i>Passer ammodendri</i>	25.54	Non-covered nest	Non-covered nest	0.616
<i>Cygnus olor</i>	25.90	Non-covered nest	Non-covered nest	0.567
<i>Oxyura vittata</i>	26.00	Non-covered nest	Non-covered nest	0.553
<i>Larus livens</i>	26.10	Non-covered nest	Non-covered nest	0.539
<i>Merops ornatus</i>	26.18	Non-covered nest	Non-covered nest	0.527
<i>Sula sula</i>	26.96	Non-covered nest	Covered nest	0.582
<i>Gallinula tenebrosa</i>	27.00	Non-covered nest	Covered nest	0.587
<i>Porphyrio porphyrio</i>	27.75	Non-covered nest	Covered nest	0.685
<i>Caiman crocodiles</i>	28.41	Covered nest	Covered nest	0.759
<i>Alligator mississippiensis</i>	29.95	Covered nest	Covered nest	0.883
<i>Scotocerca inquieta</i>	30.29	Non-covered nest	Covered nest	0.901
<i>Leipoa ocellata</i>	30.70	Covered nest	Covered nest	0.920

<i>Cygnus Cygnus</i>	32.89	Non-covered nest	Covered nest	0.975
<i>Crocodylus cataphractus</i>	33.14	Covered nest	Covered nest	0.978
<i>Crocodylus acutus</i>	34.19	Covered nest	Covered nest	0.988
<i>Alectura lathami</i>	35.92	Covered nest	Covered nest	0.995
<i>Podiceps nigricollis</i>	29.49	Unknown	Covered nest	0.853
<i>Podiceps cristatus</i>	24.19	Unknown	Non-covered nest	0.775
<i>Podilymbus podiceps</i>	35.25	Unknown	Covered nest	0.993
<i>Chlidnias niger</i>	35.67	Unknown	Covered nest	0.995

Figure 3.1: Boxplot of P_{nest} among wet aquatic nests and other nest types

Note that wet aquatic nests have a high estimated P_{nest} like covered nests.



CHAPTER FOUR: EGG WATER VAPOR CONDUCTANCE AND NEST TYPE OF LIVING ARCHOSAURS

4.1 Introduction

All living archosaurs lay rigid, calcitic eggs with eggshells that are pierced by numerous pore canals (e.g., Erben, 1970; Mikhailov, 1991) through which a certain amount of water vapor is lost by diffusion during incubation (10 to 23 % of initial egg weight in birds: e.g., Ar and Rahn, 1980; Rahn and Paganelli, 1990). The diffusive capacity of eggshell or water vapor conductance (G_{H_2O} , mgH₂O/day/Torr) of an egg is defined as the rate of water loss (i.e., water vapor diffusion) across the eggshell per unit of pressure difference of water vapor (Ar et al., 1974). Water vapor conductance of an egg is directly related to eggshell porosity and is important for regulating water loss of archosaur eggs during incubation. Because pore canals are the only pathways for gas exchange through the shell (e.g., Tazawa, 1987), pore size has a fundamental effect on G_{H_2O} (Ar et al., 1974), and G_{H_2O} is proportional to total pore area (A_p , mm²) and inversely proportional to pore length of eggshell (L_s , mm), which is expressed as,

$$G_{H_2O} = \frac{k \cdot D_{H_2O}}{R \cdot T'} \cdot \frac{A_p}{L_s} \quad (\text{Eq. 4.1})$$

where D_{H_2O} is the diffusion coefficient of water vapor (cm²/sec), k is a conversion constant (sec mg/day/mol), R is universal gas constant (cm³ Torr/mol/K), and T' is absolute temperature (K), based on the modified Fick's law of diffusion (Ar et al., 1974; Seymour, 1979).

The water loss from the egg mainly occurs due to the diffusive process of water vapor, which is caused by the pressure difference across the eggshell (Ar et al., 1974). Because absolute nest humidity (P_{nest}) is generally lower than absolute egg humidity (P_{egg} , Torr), water vapor diffuses from the egg during incubation (for review see Paganelli, 1980, 1991; Tazawa, 1987; Rahn and Paganelli, 1990). Consequently, water vapor conductance helps regulate the rate of water loss, which can be expressed as:

$$G_{H_2O} = \frac{M_{H_2O}}{P_{egg} - P_{nest}} \quad (\text{Eq. 4.2})$$

where M_{H_2O} is daily water loss (i.e., rate of water loss) of egg (mgH₂O/day) (Ar et al., 1974). Egg humidity is thought to be saturated (Taigen et al., 1978) at the optimal incubation temperature (around 34 to 38 °C) in most bird species, so P_{egg} is consistent among species between 40 and 50 Torr (Rahn, 1984; Booth and Thompson, 1991). M_{H_2O} values, relative to egg size, are also fairly consistent among bird species (personal review of the literature). Therefore, G_{H_2O} is likely to be most affected by P_{nest} , which varies considerably, and in turn affects the rate of water loss from the egg.

Because P_{nest} is an important factor that affects G_{H_2O} values (Eq. 4.2: Ar et al., 1974), G_{H_2O} should theoretically be higher in humid nests and lower in arid nests in order to avoid over humidification or desiccation of the eggs, respectively. Furthermore, G_{H_2O} values should vary with nest types, because nest humidity is correlated to nest types; P_{nest} is significantly higher in covered nests and wet aquatic nests than in other non-covered nest types (Chapters Two and Three). In fact, relatively high G_{H_2O} values for birds have been reported from unusual nesters, such as mound nesting megapodes and aquatic nesters (Lomholt, 1976; Seymour and Rahn, 1978; Ackerman and Platter-Rieger, 1979; Seymour and Ackerman, 1980; Davis et al., 1984; Sotherland et al., 1984; Ar and Rahn, 1985; Davis and Ackerman, 1985; Seymour et al., 1987). Also, relatively lower G_{H_2O} appears in scrape nesting species in arid regions (Thomas and Maclean, 1981; Rahn and Hammel, 1982; Ar and Rahn, 1985; Guerra et al., 1988; Thompson and Goldie, 1990), and in species that nest in montane regions (due to lower barometric pressure) in comparison with the same species at lower altitude (e.g., Rahn et al., 1977b; Taigen et al., 1980; Carey et al., 1983, 1989a; Leon-Velarde et al., 1984a; Carey, 2002). Such unusual nester styles are therefore likely to be outliers, from what is predicted by the strongly-correlated regression of G_{H_2O} and egg mass for bird species (Ar et al., 1974; Ar and Rahn, 1978; Hoyt, 1980; Ar and Rahn, 1985).

If a relationship between G_{H_2O} values and nest types among living birds is demonstrated, then estimates of G_{H_2O} can be used for predicting nest types in extinct archosaurs (e.g., non-avian dinosaurs, fossil birds). Although it has been speculated that G_{H_2O} values vary with respect to nest types in living birds (e.g., Seymour and Ackerman,

1980; Ar and Rahn, 1985), no statistical analysis has tested for a relationship between G_{H_2O} values and nest types in birds. Nevertheless, a number of studies have speculated nesting modes or nest types of extinct archosaurs based on estimates of G_{H_2O} values for their eggs even in the absence of demonstrated correlation between these variables (Seymour, 1979; Williams et al., 1984; Sabath, 1991; Mou, 1992; Grigorescu et al., 1994; Mikhailov et al., 1994; Sahni et al., 1994; Antunes et al., 1998; Deeming, 2006; Jackson et al., 2008, 2010; Donaire and Lopez-Martinez, 2009; Grellet-Tinner et al., 2012). Here, it is hypothesized that G_{H_2O} in birds is correlated with nest type because: 1) G_{H_2O} is affected by nest humidity (Ar et al., 1974); and 2) nest humidity is correlated with nest types (Chapters Two and Three). The purpose of this chapter is to test for differences in the regressions of G_{H_2O} and egg sizes between nest types in living bird species by using both conventional (non-phylogenetic) and phylogenetically-corrected approaches. Although analyzed in this chapter, crocodilian species were not included in the regressions because of their distant phylogenetic relationship with birds, extremely small sample size, and the questionable nature of their G_{H_2O} data.

4.2 Material and Methods

For this study, water vapor conductance of the eggs of numerous bird taxa was regressed against egg mass, eggshell surface area, and eggshell volume. Below is an explanation of the data that was used for the dependent variable (i.e., water vapor conductance of egg) and for the independent variables (i.e., egg mass, eggshell surface area, and eggshell volume). Statistical analyses were also conducted to test for significant difference of G_{H_2O} , relative to egg sizes (i.e., egg mass, eggshell surface area, and eggshell volume), between nester types, the methods of which are explained below.

4.2.1 Water Vapor Conductance

Water vapor conductance values for the eggs of 285 living bird taxa (274 species and 11 subspecies) were compiled from the literature for the purposes of this study (Appendices A and B). All values were experimentally measured in a laboratory under known temperature (usually at 25 °C) and relative humidity (usually 0 %), so in most cases the

water vapor conductance is equal to the rate of water loss divided by saturated water vapor pressure at 25 °C (Eq. 4.2). Since more than one value was usually available for a species, a mean value for G_{H_2O} was calculated. Mean values helped reduce the effects of variation, although variation in G_{H_2O} is poorly understood and can result from biological factors, environmental factors, and sampling techniques, as discussed below.

Biologically, there is natural variation in G_{H_2O} values within eggs of a clutch (Sotherland et al., 1979; Clark et al., 2010), although it is less than the variation among clutches (Sotherland et al., 1979). Known variation in G_{H_2O} among clutches of a single species may be due to individual variation of the hens (Sotherland et al., 1979), as well as differing ages (Tullett, 1981; Ancel and Girard, 1992; O'dea et al., 2004). For the data used here, it was difficult to determine how the G_{H_2O} data was gathered for an individual species for most studies so the effects of such biological variation on the data are unknown.

Barometric pressure is another factor that produces variation in G_{H_2O} values within a species (Paganelli et al., 1975; Paganelli, 1980), although most papers adjust G_{H_2O} values to approximately sea level (760 Torr). Because G_{H_2O} is proportional to barometric pressure (Paganelli et al., 1975; Carey, 1980a; Paganelli, 1980), birds that nest in high altitude generally show lower G_{H_2O} values than the same species at lower altitude, due to lower barometric pressure (e.g., Rahn et al., 1977b; Taigen et al., 1980; Carey et al., 1983, 1989a). Four species (*Agelaius phoeniceus*, *Fulica americana*, *Pica pica*, and *Turdus migratorius*) in the dataset nest from near sea level to montane regions (around 3000 m and higher), so G_{H_2O} values are standardized to sea level by the authors. Furthermore, some G_{H_2O} values for chicken (*Gallus gallus*), domesticated 400 years ago, were from nests high in the Andes (up to 3900 m) (Leon-Velarde et al., 1984a), although G_{H_2O} was measured around sea level (754 Torr).

Another potential source of variation in G_{H_2O} values can be induced by experimental conditions (e.g., temperature of desiccators). In the literature, water vapor conductance was obtained using the gravimetric technique of Ar et al. (1974) or the modified technique of Tullett (1981), which weighs daily water loss of eggs in desiccators under known temperature (most studies were at 25 °C, although some studies used other temperatures, ranging from 8 to 38 °C) and relative humidity (in most studies at 0 %) for several days. A temperature variation of desiccators itself is relatively insignificant for G_{H_2O} (e.g., only 2 %

increase in G_{H_2O} value between 25 and 37 °C: Rahn et al., 1977a). Most papers that use other temperatures adjust G_{H_2O} values to 20 to 25 °C, based on Paganelli et al. (1975).

Sampling techniques (e.g., fertile vs. infertile, and incubation period of egg) also can potentially cause variation in the G_{H_2O} values of a species, depending on the temperature of the desiccators (in some cases incubators). This is not a major issue as most values taken from the literature was sampled at 25 °C. The optimum temperature for incubation is usually around 35 °C (Drent, 1975; Webb, 1987), which permits embryonic development and thus can increase G_{H_2O} values of sampled eggs that are fertile. Although there is little variation between G_{H_2O} values of fertile and infertile eggs in some species (Kern, 1986; Booth and Rahn, 1990), G_{H_2O} values of fertile eggs were reported to increase during incubation and reach the maximum in the late stage of incubation under optimum temperature (see Deeming, 2002 for review). Here values for only 11 (*Agapornis personata*, *A. roseicollis*, *Bolborhynchus lineola*, *Coturnix coturnix*, *Enicognathus ferrugineus*, *Ficedula hypoleuca*, *Gallus gallus*, *Leipoa ocellata*, *Meleagris gallopavo*, *Serinus canaria*, and *Struthio camelus*) of the 285 taxa are reported to have come from fertile eggs with high incubation temperature (> 30 °C) and/or at a late stage of incubation. Since the mean value of G_{H_2O} was calculated for each species, a single value from these eggs in 11 of 285 taxa will not strongly affect the mean value for a given species.

For three species of birds, G_{H_2O} was obtained through other variables (i.e., M_{H_2O} and mass-specific G_{H_2O}), although G_{H_2O} was gravimetrically measured in the literature. G_{H_2O} of two grouse species (*Bonasa umbellus* and *Falcipennis canadensis*) reported by Bendell and Bendell-Young (2006) was estimated here from the M_{H_2O} regressions, which were measured under known temperature and relative humidity. Also, G_{H_2O} values of *Struthio camelus* reported by Tazawa et al. (1988) and Gefen and Ar (2001) were estimated here from mass-specific values (mgH₂O/day/Torr/g) by multiplying by egg mass (g).

G_{H_2O} for species of crocodilians were also used for comparison with birds. For three crocodilian species (*Alligator mississippiensis*, *Crocodylus acutus*, and *C. porosus*) measured G_{H_2O} was obtained from the literature (Packard et al., 1979; Lutz et al., 1980; Grigg and Beard, 1985) or calculated using data from the literature. However, the accuracy of G_{H_2O} measured for crocodilians has been questioned (Grigg and Beard, 1985). G_{H_2O} of *C. porosus* was calculated here based on daily water loss of egg and known humidity from

Grigg and Beard (1985) and include data from both infertile and fertile eggs of the late incubation period with 30 °C temperature, fertile eggs of which potentially could increase G_{H_2O} values (see above). However, a mean value was also used for this taxon.

4.2.2 Egg Mass

Egg mass (M, g) could be obtained from the literature for 278 taxa of the 285 taxa for which G_{H_2O} was available. In cases where M is not provided with a G_{H_2O} value, M was obtained from other papers (i.e., for *Anas carolinensis*, *A. melleri*, *Apteryx australis*, *Merganetta a. armata*, *Oceanodroma furcata*, *Pica pica*, *Serinus canaria*, *Sylvia curruca*, and *Xanthocephalus xanthocephalus*). *Phoenicopterus andinus* (Andean Flamingo) was excluded from the regression of G_{H_2O} and egg mass because the correct egg mass could not be found in the literature. Egg mass for *P. andinus* (29 g) reported from French and Board (1983) is likely incorrect, based on comparison of reported masses for other flamingo species, which have similar egg length and breadth [e.g., 115 g (78 × 49 mm) for *P. minor* and 140 g (90 × 55 mm) for *P. roseus* (del Hoyo et al., 1992) vs. 89 × 54.3 mm for *P. andinus* (Schonwetter, 1960-1967)].

4.2.3 Eggshell Surface Area

Surface area (A_s , mm²) of the eggs could be calculated for 284 taxa of the 285 taxa for which G_{H_2O} is known. This independent variable was calculated from egg length (L, mm) and breadth (B, mm) ($L \geq B$), which were obtained from various sources (primarily from Schonwetter, 1960-1967). For the eggs of all bird species, an equation for surface area derived from the domestic chicken (Narushin, 2005),

$$A_s = (3.155 - 0.0136 \cdot L + 0.0115 \cdot B) \cdot L \cdot B \quad (\text{Eq. 4-3})$$

was used, with an assumption that this formula is applicable for bird eggs in general. Eggs of crocodilians were assumed to be prolate spheroid in shape, so a general equation of prolate spheroid surface area was used as follows:

$$A_s = 2 \pi \cdot (L'^2 + L' \cdot B' \cdot \frac{\alpha}{\sin \alpha}) \quad (\text{Eq. 4.4})$$

where $L' = L / 2$, $B' = B / 2$, and angular eccentricity $\alpha = \arcsin (L' / B')$.

4.2.4 Eggshell Volume

Eggshell volume (V_{shell} , mm^3) could be estimated for 234 taxa (228 species and six subspecies) of the 285 taxa for which $G_{\text{H}_2\text{O}}$ is known. Although M and A_s have been traditionally used to examine a relationship with $G_{\text{H}_2\text{O}}$ (e.g., Paganelli et al., 1975; Carey et al., 1983, 1990; Leon-Velarde et al., 1984a, 1984b; Arad et al., 1988; Ancel and Girard, 1992; Conway, 1998), V_{shell} is also appropriate because it considers both egg size and pore length through which water vapor diffuses. Eggshell volume for each taxon was calculated by multiplying A_s by pore length (L_s , mm).

Pore length was considered equal to shell thickness, based on the assumptions by Ar et al. (1974) and Ar and Rahn (1985). Shell thickness, as a proxy for pore length, of the 234 bird taxa and three crocodilian species was obtained from the literature and from personal observations (Table 4.1). It was assumed that regional differences within an egg had little effect on shell thickness. For megapode species (*Alectura lathamii* and *Leipoa ocellata*), L_s was averaged between early and late incubation periods because L_s becomes significantly shorter during incubation (Booth and Seymour, 1987; Booth and Thompson, 1991). Personal observation of shell thickness includes specimens from the ROM (Royal Ontario Museum, Toronto) and ZEC (Zelenitsky Egg Catalogue, the University of Calgary, Calgary), measured by a Mitutoyo micrometer CPM30-25MJ (permissible value $\pm 2 \mu\text{m}$).

4.2.5 Nester Type Classification

All 285 bird taxa examined in this chapter were classified as either a humid (species which build covered nests or non-covered wet aquatic nests) or regular nester (species which build non-covered nests, excluding wet aquatic nests), based on nest humidity and the nest type classification. Because nest humidity is correlated to nest types (i.e., covered and non-covered wet aquatic nests have a high P_{nest} ; non-covered nests have a low P_{nest} : Chapters Two and Three), each taxon could be assigned to either humid or regular nester

based on nest information (e.g., nest structure and nest location) derived from the literature (e.g., Harrison, 1975; Baicich and Harrison, 1997), the classification schemes of nest structure and location of Hansell (2000), or nest humidity. Humid nesters thus correspond to species with a high P_{nest} , whereas regular nesters have a low P_{nest} . For three species in which the nest structure is poorly known (i.e., *Anas sibilatrix*, *Bolborhynchus lineola*, and *Dendrocygna guttata*), nest structure of a related species (within the same genus) was used.

4.2.6 Statistical Analysis (ANCOVA)

Water vapor conductance of the eggs of humid and regular bird nesters was compared by analysis of covariance (ANCOVA), using phylogenetic and non-phylogenetic approaches. Non-phylogenetic approach (i.e., conventional approach) refers to a general statistical method that does not take into account the phylogenetic relationship of the data points, and assumes that data points (i.e., taxa) for the regression are statistically independent each other (see Garland et al., 2005 for review). This assumption is not entirely correct because data points representing taxa are all interrelated due to an evolutionary history (Garland et al., 2005), and a fallacious assumption may inflate the rate of Type I error, which wrongly detects a statistical significance. Thus for this study, a phylogenetically-corrected approach, which uses the independent contrast method (Felsenstein, 1985), was also applied to the ANCOVA, so the phylogenetic relationship of the data points is considered. Regression models generated by both approaches (i.e., conventional and phylogenetically corrected) were then analyzed with Akaike Information Criterion in order to examine which regression model represents a better fit.

Before all the analyses, the variables ($G_{\text{H}_2\text{O}}$, M , A_s , and V_{shell}) were transformed into 10-based logarithms, which is an appropriate method because logarithmic distribution is commonly seen in nature, normalizes distribution, reduces the effect of outliers, and maintains homoscedasticity (e.g., Martin, 1981; Smith, 1984, 1993). For ANCOVAs, $G_{\text{H}_2\text{O}}$ was used as the dependent variable, whereas M , A_s , and V_{shell} were covariates.

4.2.6.1 Conventional Approach: Non-Phylogenetically Corrected Regressions

As a conventional approach (i.e., general statistical approach), ordinary least-squares

(OLS) regression was conducted for both humid and regular bird nesters. Slopes and intercepts were provided with the 95 % confidence intervals.

Regressions of humid and regular bird nesters were then compared by conventional ANCOVA (i.e., non-phylogenetically corrected ANCOVA or non-pc ANCOVA), which first tests the homogeneity of slopes and then the intercepts between the two groups. Before the analysis, Shapiro-Wilk tests for normal distribution of log G_{H2O} residuals, and Levene tests for the equality of variances were performed in order to confirm whether parametric ANCOVA was appropriate. Residuals of log G_{H2O} for each species were calculated based on regression lines of each bird nester (humid and regular nesters) for the Shapiro-Wilk tests. All statistical analyses for non-phylogenetically corrected approaches were conducted with IBM SPSS Statistics v. 19.0.0 (SPSS, Inc.).

4.2.6.2 Phylogenetically-corrected Approach: Regressions with Phylogenetic Model

Regressions of humid and regular bird nesters were then generated with a phylogenetically-corrected approach. For phylogenetically-corrected analyses, a phylogenetic tree of 285 species and subspecies of living birds was reconstructed, using Hackett et al. (2008) for a large-scale phylogeny and other papers for interrelationships within each order (Appendix C). Most papers, which were published recently (after 2000), provide molecular phylogenies, but morphological phylogenies were also used when molecular were unavailable. Due to unresolved phylogenetic relationships of some taxa and inconsistencies in phylogenetic hypotheses among papers, the reconstructed supertree of bird species has 31 unresolved polytomies. Because the tree was a composite of various sources, arbitrary branch length models were used by following a procedure of Garland et al. (1992). Adequate standardized branch lengths were obtained by Grafen's (1989) Rho transform method ($\rho = 0.5$). The phylogenetic tree was reconstructed with PDAP module v. 1.15 (Midford et al., 2010) of the software Mesquite v. 2.73 (Maddison and Maddison, 2010).

Phylogenetically-corrected ANCOVA (i.e., pc ANCOVA) were then implemented following the method of Lavin et al. (2008). Briefly, a character matrix and phylogenetic variance-covariance matrix were generated with PDAP module in Mesquite and DOS PDDIST program (Garland and Ives, 2000), respectively. Phylogenetically-corrected

ANCOVA were tested with MATLAB program Regressionv2.m (available from T. Garland Jr.). Non-pc (conventional) ANCOVA was also implemented by Regressionv2.m in order to confirm the results of IBM SPSS. Regressions of OLS on scatter plots were plotted by IBM SPSS because Regressionv2.m does not generate a graph for PGLS and RegOU regressions.

Phylogenetically-corrected regressions included two different evolutionary models: Brownian motion and Ornstein-Uhlenbeck models (e.g., Lavin et al., 2008; Hall et al., 2009; Swanson and Garland, 2009; Garland et al., 2010). Regressions with Brownian motion model (i.e., phylogenetic generalized least-squares, or PGLS) assume an evolutionary process with “random walk in continuous time” (e.g., Lavin et al., 2008), whereas regressions with Ornstein-Uhlenbeck model (i.e., phylogenetic regression with Ornstein-Uhlenbeck process, or RegOU) assume an evolutionary process of “wandering back and forth on a selective peak” (Felsenstein, 1988; Butler and King, 2004; Lavin et al., 2008). For pc ANCOVA, nester type (i.e., humid and regular nesters) was included as a categorical variable (i.e., humid nester = 1 and regular nester = 2), as was each covariate (i.e., $\log M$, $\log A_s$, and $\log V_{\text{shell}}$). Thus, two different regression models (PGLS and RegOU) for three different covariates ($\log M$, $\log A_s$, and $\log V_{\text{shell}}$) were applied for pc ANCOVA.

4.2.6.3 Comparisons between Conventional and Phylogenetically-Corrected

Regressions

Conventional (OLS) and phylogenetically-corrected regressions (PGLS and RegOU) were compared with Akaike Information Criterion (AIC) to determine a better fit model of regression. Values of AIC are commonly used for evaluation of regression models (e.g., Spoor et al., 2007; Lavin et al., 2008; Warne and Charnov, 2008; Gutierrez-Ibanez et al., 2009; Hall et al., 2009; Swanson and Garland, 2009; Gartner et al., 2010; Lovegrove, 2010; Lovegrove et al., 2011; Swanson and Bozinovic, 2011); a lower value indicates a better fit of model. If AIC values are lower in phylogenetically-corrected (PGLS or RegOU) regressions than in the conventional (OLS) regressions, it can imply that there is “phylogenetic signal” in the data (Blomberg and Garland, 2002; Blomberg et al., 2003;

Garland et al., 2010). AIC values for all regression models (i.e., OLS, PGLS, and RegOU) were calculated with Regressionv2.m program.

4.3 Results

4.3.1 Nest Classification

To assess the relationships between G_{H_2O} values and nesting modes of living birds, 285 taxa of birds were classified into either humid or regular nesters (Table 4.2; Appendix D). Eight species were classified as humid nesters, which include mound nesting megapodes (*Alectura lathami* and *Leipoa ocellata*) and six species of aquatic birds (i.e., *Gavia immer*, *Chlidonias niger*, and four species of grebes) known to build wet aquatic nests (Roberts, 1936; Bent, 1963; Bergman et al., 1970; Lomholt, 1976; Terres, 1980; Davis et al., 1984; Southerland et al., 1984; Storer and Nuechterlein, 1992; Dunn and Agro, 1995; McIntyre and Barr, 1997; Muller and Storer, 1999). Regular nesters include 277 taxa, which build nests of a variety of uncovered nest architectures in various locations in a wide range of habitats, including severe dry environments, such as true deserts (e.g., *Ammoperdix heyi*, *Larus modestus*, *P. namaqua*, *Pterocles orientalis*, *Struthio camelus*) and polar regions (e.g., *Aptenodytes patagonicus* and *Pygoscelis adeliae*) (del Hoyo et al., 1992; Dean, 2004).

4.3.2 Water Vapor Conductance and Egg Sizes of Humid and Regular Nesters

Based on the literature, G_{H_2O} values for 285 taxa of living birds were compiled for this study (Appendices A and B). Means and ranges of G_{H_2O} values and egg sizes (i.e., M , A_s , and V_{shell}) for each nester type are shown in Table 4.3.

4.3.3 Conventional ANCOVA

Egg water vapor conductance of humid and regular bird nesters was strongly correlated with egg mass, eggshell surface area, and eggshell volume (each with a $r^2 > 0.79$: Table 4.4; Figs. 4.1 to 4.3). The 95 % confidence intervals of each slope and intercept

partially overlapped between regressions of humid and regular nesters for each independent variable (Table 4.4). Humid nesters showed relatively higher G_{H_2O} values than regular nesters, and most humid nesters plotted above the 95 % confidence interval of regular nesters (Figs. 4.4 to 4.6). Among regular nesters, some desert and polar species, such as *Struthio camelus*, *Ammoperdix heyi*, *Pterocles orientalis*, *Aptenodytes patagonicus*, *Pygoscelis adeliae*, and *Larus modestus*, showed comparatively low G_{H_2O} values (Figs. 4.4 to 4.6).

Ordinary least-square regressions of humid and regular bird nesters were tested by conventional ANCOVAs. Before the analyses, distributions of $\log G_{H_2O}$ residuals for each nester type (humid and regular) and the variances between two nester types were examined by Shapiro-Wilk tests and Levene tests, respectively; distributions of all groups were not significantly non-normal (in all cases $p \gg 0.05$ except one case $p = 0.043$) and the equality of variances can be assumed among all cases ($p \gg 0.05$) (Table 4.5). Thus, assumptions of ANCOVA were safely met. Conventional ANCOVAs revealed that slopes were not significantly different between humid and regular nesters (in all cases $p > 0.05$; Table 4.6). However, intercepts were significantly higher in humid nesters than in regular nesters (in all cases $p \ll 0.05$). These results were corroborated by regressions with all different covariates (i.e., $\log M$, $\log A_s$, and $\log V_{shell}$).

4.3.4 Phylogenetically-Corrected ANCOVA

Phylogenetically-corrected ANCOVAs also revealed significant differences of G_{H_2O} between humid and regular nesters (in all cases $p \ll 0.05$; Table 4.7). All regression models tested here (i.e., PGLS and RegOU with three different covariates, including $\log M$, $\log A_s$, and $\log V_{shell}$) corroborated the results of conventional ANCOVAs.

4.3.5 Comparisons between Conventional and Phylogenetically-Corrected Regressions

Conventional (OLS) and phylogenetically-corrected regressions (PGLS and RegOU) were compared by Akaike Information Criterion. Among all models with different covariates (i.e., $\log M$, $\log A_s$, and $\log V_{shell}$), all RegOU models showed lower AIC values than OLS and PGLS models, indicating RegOU models are better fits than the others. The

lowest AIC value, which indicates the best fit of regression models, was seen in RegOU with log M as a covariate (Table 4.7). Thus, this implies that a phylogenetic signal is present in the dataset.

4.3.6 Water Vapor Conductance and Egg Size of Crocodilians

Values of G_{H_2O} from three crocodilian species (*Alligator mississippiensis*, *Crocodylus acutus*, and *C. porosus*; Appendices A and B) were compared with those of bird nesters. Means and ranges of G_{H_2O} , M, A_s , and V_{shell} of the crocodilians are shown in Table 4.8. G_{H_2O} values of crocodilian species are relatively high, compared with most bird species (Figs. 4.4 to 4.6; Appendices A and B). In the three OLS regressions (i.e., M, A_s , and V_{shell} as independent variables) of bird species, *A. mississippiensis* plots above the regressions of bird humid nesters, although the other two crocodilian species plotted between the regressions of humid and regular bird nesters, except for one data point of *C. porosus*, which is above the regression of humid bird nesters (Fig. 4.4).

4.4 Discussion

4.4.1 Egg Water Vapor Conductance of Living Archosaurs

This chapter represents the most comprehensive study of its type in that it uses more than 550 values of 285 taxa to compare G_{H_2O} values among the eggs of living birds, which is a significantly greater than all previous datasets. Although it has been speculated that G_{H_2O} may vary among nest types (e.g., Seymour, 1979; Seymour and Ackerman, 1980; Ar and Rahn, 1985; Jackson et al., 2008), this study is the first to search for correlations between nester types (i.e., humid and regular) and G_{H_2O} values for birds using statistical methods. This study shows that G_{H_2O} values are significantly different among these nesters.

Two nester types (humid and regular nesters) were established for this chapter, based on nest architectures/types (covered, non-covered wet aquatic, and other non-covered nests), which are shown to have a significantly different absolute nest humidity (Chapters Two and Three). Although aquatic nests are also common in several taxa of waterbirds (e.g., swans, ducks, coots, swamphens, and moorhens) (Harrison, 1975; Lill, 1990; del Hoyo et al., 1992;

Baicich and Harrison, 1997; Brisbin et al., 2002), wet nest materials are usually only used by *Chlidonias niger* (Black Tern), *Gavia immer* (Common Loon) and grebe species in the dataset. In this chapter, humid nesters are shown to have a significantly higher water vapor conductance, relative to egg size (i.e., M , A_s , and V_{shell}), than in regular nesters, as shown by both conventional and phylogenetically-corrected ANCOVA methods.

The differences of G_{H_2O} between two nester types can be explained by the humidity gradient between the eggs and the nests ($P_{egg} - P_{nest}$). Although P_{egg} is likely to be constant in all bird species around 40 to 50 Torr due to a consistent incubation temperature in birds (around 34 to 38 °C) (Booth and Thompson, 1991), P_{nest} is significantly higher in humid nesters than in regular nesters (Chapters Two and Three). As a consequence, the gradient between P_{egg} and P_{nest} is less in humid nesters than in regular nesters. Thus, eggs of regular nesters tend to lose water at a greater rate than the eggs of humid nesters. In order to avoid over desiccation or over humidification of the eggs for regular and humid nesters, respectively, G_{H_2O} should be lower in regular nesters and higher in humid nesters (Eq. 4.2).

Although G_{H_2O} values are usually regressed against egg mass or eggshell surface area in the literature, the use of eggshell volume as an independent variable is unique to this study. In previous studies, egg mass or surface area are commonly used for comparisons of G_{H_2O} values among/within species, as mass-specific G_{H_2O} and permeability of the eggshell, respectively (e.g., Paganelli et al., 1975; Carey et al., 1983, 1990; Leon-Velarde et al., 1984a, 1984b; Arad et al., 1988; Ancel and Girard, 1992; Conway, 1998). Eggshell volume as used here, however, is appropriate because it considers both eggshell surface area and shell thickness (= pore length), through which the water vapor diffuses. In fact, $\log V_{shell}$ is strongly correlated to $\log G_{H_2O}$, with high r^2 values (> 0.91) (Table 4.4), so is a useful independent variable for comparison of G_{H_2O} values among species.

This is also the first study to use the phylogenetically-corrected method for analyses of allometric relationships between G_{H_2O} and egg size. Because the phylogenetically-corrected method considers evolutionary history of taxa (i.e., data points), it can avoid inflation of a Type I error, which could be induced by an assumption that data points are independent of each other in OLS (Felsenstein, 1985; Harvey and Pagel, 1991; Garland and Adolph, 1994; Garland et al., 2005). In fact, in this study, Akaike Information Criterion suggested that a phylogenetic model (i.e., RegOU) is a better fit than

non-phylogenetic model (i.e., OLS regressions).

4.4.2 Adaptations of Humid Nesters

High G_{H_2O} values of humid nesters are achieved by varying eggshell characteristics. High G_{H_2O} values result from large total pore area (A_p , mm²) and/or small L_s values (Tullett and Board, 1977) because G_{H_2O} is proportional to A_p and inversely proportional to L_s , based on the modified Fick's law of gas diffusion (Eq. 4.1; Ar et al., 1974). Total pore area is determined by multiplication of mean cross-sectional individual pore area (A , mm²) and total number of pores per egg (N). Aquatic nesters, such as *Chlidonias niger*, *Gavia immer*, and grebes, achieve high G_{H_2O} values by increasing N , rather than by increasing A or decreasing L_s (Tullett and Board, 1977; Ackerman and Platter-Rieger, 1979; Davis et al., 1984; Ar and Rahn, 1985; Davis and Ackerman, 1985). However, mound nesting megapodes achieve high G_{H_2O} values by decreasing L_s . *Alectura lathamii* and *Leipoa ocellata* have considerably thinner eggshell than predicted for the egg size (Seymour and Rahn, 1978; Booth and Seymour, 1987; Seymour et al., 1987; Seymour and Ackerman, 1980). Furthermore, pore length decreases 12 % in *A. lathamii* and 21 % in *L. ocellata* by calcium absorption of embryos through incubation, and G_{H_2O} eventually increases three-fold at the end of incubation in *L. ocellata* (Booth and Seymour, 1987; Booth and Thompson, 1991) to satisfy the oxygen demand by the developing embryo in underground nest environment (i.e., high carbon dioxide and low oxygen tensions) (Booth and Seymour, 1987; Seymour et al., 1987; Booth and Thompson, 1991).

4.4.3 Adaptation to Drier Nesting

Although nester types were classified into only two types (i.e., regular and humid) for this chapter, regular nesters include some species that show lower G_{H_2O} values (Figs. 4.4 to 4.6). In the dataset, *Struthio camelus*, *Ammoperdix heyi*, *Pterocles orientalis*, *P. namaqua*, and *Larus modestus* inhabit true deserts, where annual precipitation is less than 250 mm (Dean, 2004). Also, two penguin species, *Aptenodytes patagonicus* and *Pygoscelis adeliae* breed in Antarctic regions, where ambient humidity is extremely low (e.g., 6.8 Torr in a nest site of *A. patagonicus*: Handrich, 1989) due to low air temperature (-4 to 10 °C in the

nesting season: Rahn and Hammel, 1982; Handrich, 1989). These species build scrape nests without nest materials, except *A. patagonicus*, which broods eggs between the parent's feet (Appendix D). Due to low ambient humidity, P_{nest} of these desert species and penguins also should be very low because P_{nest} of scrape nests is only about 5 Torr higher than ambient humidity (Deeming, 2011; see also Chapter Two). As a consequence, the humidity gradient between P_{egg} and P_{nest} would be large, and their $G_{\text{H}_2\text{O}}$ values appear to be relatively low, for regular nesters (Figs. 4.4 to 4.6).

Eggs of dry nesters attain a low $G_{\text{H}_2\text{O}}$ either through reduced N and A_p , and/or presence of thick organic layer covering the outer surface of the eggshell. Total number of pores per egg is much reduced in *Ammoperdix heyi* and *Pterocles orientalis* (Ar and Rahn, 1985), and A_p is decreased in *Larus modestus* (Monge et al., 2000). Due to complex branching structure of the pore system, N and A_p of the eggs of *Struthio camelus* are difficult to measure, although Christensen et al. (1996) reported that observed N is lower than the prediction based on other species. In *Aptenodytes patagonicus* and *Pygoscelis adeliae*, reduced pore size and presence of the organic cuticle layer on eggshell surface helps decrease of $G_{\text{H}_2\text{O}}$ values (Rahn and Hammel, 1982; Handrich, 1989; Thompson and Goldie, 1990). The organic cuticle layer in these species covers the entire shell surface, including pore openings, and is less than 50 μm in thickness, but comprises 4 to 8 % of shell thickness (Tyler, 1965; Handrich, 1989; Thompson and Goldie, 1990). Experiments by Handrich (1989) and Thompson and Goldie (1990) indicate that the $G_{\text{H}_2\text{O}}$ of the eggs increase by approximately 20 % after removal of organic layer.

4.4.4 Water Vapor Conductance of Crocodilian Eggs

Mean $G_{\text{H}_2\text{O}}$ of the eggs of living crocodilians tends to be high in comparison to bird eggs, although there is a large variation of values between fertile and infertile eggs (Figs. 4.4 to 4.6). Experiments of *Crocodylus porosus* show that $G_{\text{H}_2\text{O}}$ is three to four times higher in fertile eggs than in infertile eggs, although the reason is not understood (Grigg and Beard, 1985). Regardless of this variation between fertile and infertile eggs, the mean $G_{\text{H}_2\text{O}}$ value of *C. porosus* is as high as birds that are classified as humid nesters (Figs. 4.4 to 4.6). Among the three crocodilian species, the mean $G_{\text{H}_2\text{O}}$ value of *Alligator mississippiensis* was the highest, which was measured from only fertile eggs with early incubation period

(Packard et al., 1979), and each data point plots above the regression lines of humid nester bird species (Figs. 4.4 to 4.6). In contrast, *C. acutus* was sampled only from infertile eggs, and the measured G_{H_2O} value is as low as regular nester bird species (Figs. 4.4 to 4.6; Lutz et al., 1980). Thus, the G_{H_2O} of crocodilian species appears to vary greatly between fertile and infertile eggs, although the mean values of fertile and infertile eggs are comparable to humid nester bird species.

Although there is a large variation of crocodilian G_{H_2O} between fertile and infertile eggs, values are relatively stable during incubation (Grigg and Beard, 1985; Kern and Ferguson, 1997). Statistical tests suggest that eggs of *C. porosus* lose water at the same rate in desiccators among different incubation periods (Grigg and Beard, 1985). This was not expected in crocodilian eggs (Grigg and Beard, 1985), because the eggshell porosity allegedly increases through incubation, according to the observations of *A. mississippiensis* by Ferguson (1981). If crocodilian eggshell truly does become more porous during incubation, G_{H_2O} values should also increase. Currently no study has approached this contradiction, and further investigation is required for argument of the factors that affect G_{H_2O} values among crocodilian eggs.

4.4.5 Reconstruction of Nesting Types/Modes of Extinct Archosaurs Using G_{H_2O}

As shown in this thesis, G_{H_2O} values and nest humidity of living archosaur species are significantly different between nester types. Thus, estimations of G_{H_2O} values could potentially be used to predict unknown nest types of archosaur species, including those of extinct taxa (e.g., non-avian dinosaurs and extinct birds). The results show high G_{H_2O} values indicate a humid, covered nest or wet aquatic nest, whereas a low value indicates a non-covered nest type. G_{H_2O} values are not implicative for nest location so differentiating covered nests from floating aquatic nests in extinct taxa would have to be done with taphonomical or sedimentological evidence. However, it is highly unlikely that non-avian dinosaurs built wet aquatic nests, although they could occur for highly aquatic extinct birds.

G_{H_2O} estimations for extinct taxa are complicated by the use of different methods of estimation from those used for living taxa. The methodology to estimate G_{H_2O} values in living taxa is experimental (i.e., gravimetric method: Ar et al., 1974), whereas in extinct taxa a porosity estimation is required and a formula developed from the Fick's law of gas

diffusion is used (E.q. 4.1; Ar et al., 1974; Seymour, 1979):

$$G_{H_2O} = \frac{k \cdot D_{H_2O}}{R \cdot T'} \cdot \frac{A_p}{L_s}$$

Certain assumptions have been made for estimating G_{H_2O} for the eggs of fossil taxa in that: incubation temperature is assumed to be similar to that of birds (30 °C), barometric pressure of the nest site is assumed to be near sea level (760 Torr), the diffusion coefficient of water vapor in air is assumed to be the same in the Jurassic and Cretaceous atmosphere, and the effect of the eggshell organic materials on water vapor conductance is ignored because the organic material is generally not fossilized. The acceptance of such assumptions occurs throughout the literature where this formula is applied (Seymour, 1979; Williams et al., 1984; Sabath, 1991; Mou, 1992; Grigorescu et al., 1994; Mikhailov et al., 1994; Sahni et al., 1994; Antunes et al., 1998; Deeming, 2006; Jackson et al., 2008; Donaire and Lopez-Martinez, 2009; Grellet-Tinner et al., 2012). One further issue is that no study has tested if non-experimental G_{H_2O} values (i.e., based on the formula above) are even statistically similar to the actual experimental measurements (i.e., gravimetric method) of G_{H_2O} values among living taxa. Thus, it remains unknown if the theoretical formula is an accurate estimator for actual G_{H_2O} values in the eggs of living archosaurs, yet this formula is used widely to estimate G_{H_2O} values in the eggs of extinct taxa. Other factors relating to preservation of fossilized eggs, such as egg size, shell thickness, pore size and geometry, create further complications as accurate measurements of these features should be used to estimate G_{H_2O} , although the preservation of these fossils can be poor.

In summary, this chapter shows that G_{H_2O} values are correlated with nest types among living archosaurs, which was previously unknown but just assumed. However, although G_{H_2O} estimations in extinct archosaur eggs have been used widely to predict nest types/modes, there are several assumptions and unknowns related to the theoretical formula used to estimate G_{H_2O} values for extinct archosaurs. Future work needs to explore the accuracy of G_{H_2O} estimations in extinct taxa, and investigations of other methods or techniques should be conducted to help determine nest types in extinct archosaurs.

Table 4.1: Eggshell thickness measured in living archosaurs, as a proxy for pore length

Catalogue #	<i>Species</i>	L_s (mm)
ROM 230	<i>Carduelis tristis</i>	0.065
ROM5 224	<i>Fulica atra</i>	0.265
ROM 12701	<i>Junco hyemalis</i>	0.074
ROM 5326	<i>Limosa limosa</i>	0.197
ROM 217	<i>Molothrus ater</i>	0.129
ROM 3768	<i>Numenius arquata</i>	0.238
ROM 101	<i>Podiceps cristatus</i>	0.264
ROM 3657	<i>Tringa totanus</i>	0.162
ROM 11550	<i>Vanellus vanellus</i>	0.183
ZEC 238	<i>Crocodylus porosus</i>	0.386

Table 4.2: Nest architecture and P_{nest} of humid and regular nester types in bird species

Nester type	n	Nest shape	Nest location	P_{nest}	Remarks
Humid	8	Mound (covered)	On the ground	High	Wet nest material
		Bed (non-covered)	On water	Possibly high	Wet nest material
Regular	277	Various shapes (non-covered)	Various locations	Relatively low	Includes species in arid regions

Table 4.3: Descriptive statistics of G_{H_2O} values and egg size variables for bird species

Note that regular and humid nesters show different means and ranges. SD indicates standard deviation.

Variable	Type	n	Minimum	Maximum	Mean	SD
G_{H_2O} (mgH ₂ O/day/Torr)	Regular nesters	277	0.210	152.537	11.175	14.749
	Humid nesters	8	3.740	98.000	32.033	30.924
M (g)	Regular nesters	270	0.860	1487.494	69.622	119.110
	Humid nesters	8	10.610	194.000	83.160	76.652
A_s (mm ²)	Humid nesters	8	2528.490	14304.840	7955.776	5034.745
	Regular nesters	276	456.320	50797.290	6687.195	5243.149
V_{shell} (mm ³)	Regular nesters	226	26.180	95702.100	3036.101	7105.264
	Humid nesters	8	328.700	7811.310	2715.099	2504.573

Table 4.4: OLS regression statistics for G_{H_2O} and egg size variables in humid and regular nesters

Note that G_{H_2O} is strongly correlated with egg sizes (M , A_s , and V_{shell}) ($p \ll 0.001$). CI indicates 95 % confidence intervals.

Nester type	n	Covariate	Slope	CI of slope	Intercept	CI of intercept	r^2	p
Regular nester	271	$\log M$	0.836	0.807 – 0.865	-0.465	-0.513 – -0.418	0.920	$\ll 0.001$
Regular nester	276	$\log A_s$	1.050	0.985 – 1.114	-3.063	-3.301 – -2.825	0.791	$\ll 0.001$
Regular nester	226	$\log V_{shell}$	0.782	0.751 – 0.814	-1.624	-1.724 – -1.523	0.914	$\ll 0.001$
Humid nester	8	$\log M$	0.890	0.588 – 1.191	-0.203	-0.736 – 0.331	0.897	$\ll 0.001$
Humid nester	8	$\log A_s$	1.461	0.994 – 1.927	-4.254	-6.038 – -2.469	0.907	$\ll 0.001$
Humid nester	8	$\log V_{shell}$	1.011	0.878 – 1.143	-1.972	-2.407 – -1.537	0.983	$\ll 0.001$

Table 4.5: Results of (A) Shapiro-Wilk test and (B) Levene test of the dataset in Chapter Four

The results indicate there is no significant differences in all tests ($p > 0.05$ except one case* $p > 0.01$), which allows using ANCOVA. Residuals of $\log G_{H_2O}$ were calculated based on regressions of humid and regular nesters, which were estimated in Table 4.4. Parenthesis indicates independent variables used for the tests.

(A)

Residual type	n	W value	p
Residual of regular nesters based on M	268	0.990	0.071
Residual of regular nesters based on A_s	276	0.990	0.069
Residual of regular nesters based on V_{shell}	226	0.987	0.043*
Residual of humid nesters based on M	8	0.916	0.401
Residual of humid nesters based on A_s	8	0.917	0.403
Residual of humid nesters based on V_{shell}	8	0.946	0.668

(B)

Test	d.f.	F value	p
Regular vs. humid nesters (log M)	1, 276	0.168	0.682
Regular vs. humid nesters (log A_s)	1, 282	0.015	0.904
Regular vs. humid nesters (log V_{shell})	1, 232	0.793	0.374

Table 4.6: Results of conventional ANCOVAs

Significant differences occur between G_{H_2O} values of humid and regular nesters (significance at least at 0.01). Parenthesis indicates covariates of each regression.

Combinations	Slope			Intercept		
	d.f.	F value	p	d.f.	F value	p
Regular vs. humid nesters (log M)	1, 274	0.135	0.714	1, 275	56.793	4.988×10^{-12}
Regular vs. humid nesters (log A_s)	1, 280	0.414	0.520	1, 281	52.077	7.028×10^{-13}
Regular vs. humid nesters (log V_{shell})	1, 230	3.505	0.062	1, 231	60.078	2.881×10^{-13}

Table 4.7: Results of phylogenetically-corrected ANCOVAs and AIC values

Three regression models (OLS, PGLS, and RegOU) include three different independent variables (M, A_s , and V_{shell}) with a categorical variable (i.e., nester types). The ANCOVAs indicate that there are significant differences of $G_{\text{H}_2\text{O}}$ between humid and regular nesters ($p \ll 0.01$) in all regression models (the table also show the results of OLS, taken from Table 4.6). The lowest AIC is seen in the regression of RegOU with log M model (bold), which suggests the best fit model.

Regression model	Covariate	d.f.	F value	p	AIC value
OLS + nester types	log M	1, 275	56.793	$\ll 0.01$	-336.30
	log A_s	1, 281	52.077	$\ll 0.01$	-314.23
	log V_{shell}	1, 231	60.078	$\ll 0.01$	-245.20
PGLS + nester types	log M	1, 275	51.246	$\ll 0.01$	-322.88
	log A_s	1, 281	46.406	$\ll 0.01$	-309.32
	log V_{shell}	1, 231	53.383	$\ll 0.01$	-226.13
RegOU + nester types	log M	1, 275	50.268	$\ll 0.01$	-368.62
	log A_s	1, 281	45.821	$\ll 0.01$	-348.76
	log V_{shell}	1, 231	52.862	$\ll 0.01$	-265.16

Table 4.8: Descriptive statistics of G_{H_2O} values and egg sizes in crocodilian species

The results show relatively high water vapor conductance. SD indicates standard deviation.

Variable	n	Minimum	Maximum	Mean	SD
G_{H_2O} (mgH ₂ O/day/Torr)	3	21.000	51.593	34.810	15.512
M (g)	3	72.270	80.000	76.858	4.063
A_s (mm ²)	3	8743.419	11477.825	9668.082	1567.409
V_{shell} (mm ³)	3	3077.683	5269.801	4259.308	1106.033

Figure 4.1: Scatter plot and OLS regressions of $\log G_{H_2O}$ and $\log M$ between humid and regular nesters

Note that the regression of humid nesters is above that of regular nesters.

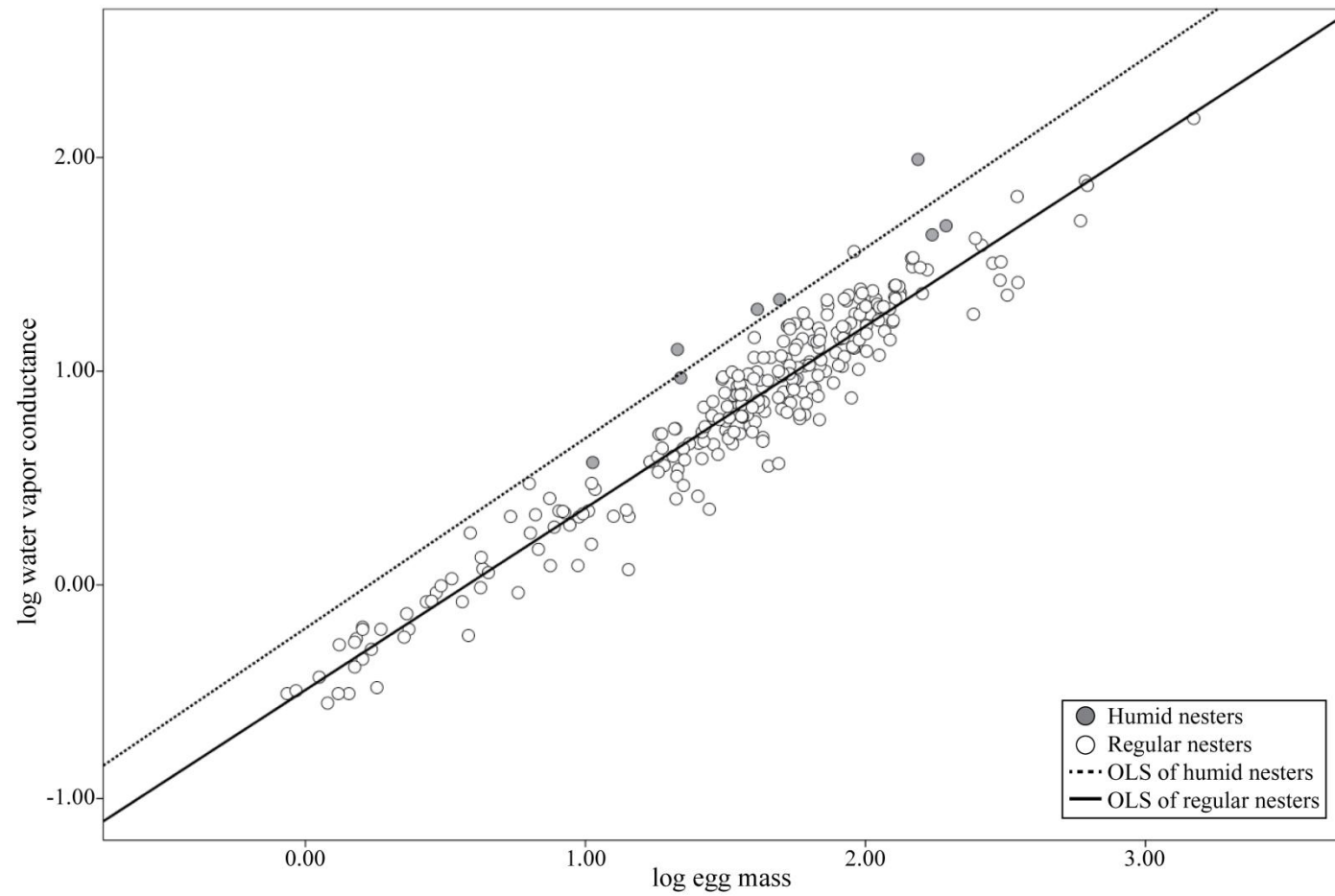


Figure 4.2: Scatter plot and OLS regressions of $\log G_{H_2O}$ and $\log A_s$ between humid and regular nesters

Note that the regression of humid nesters is above that of regular nesters.

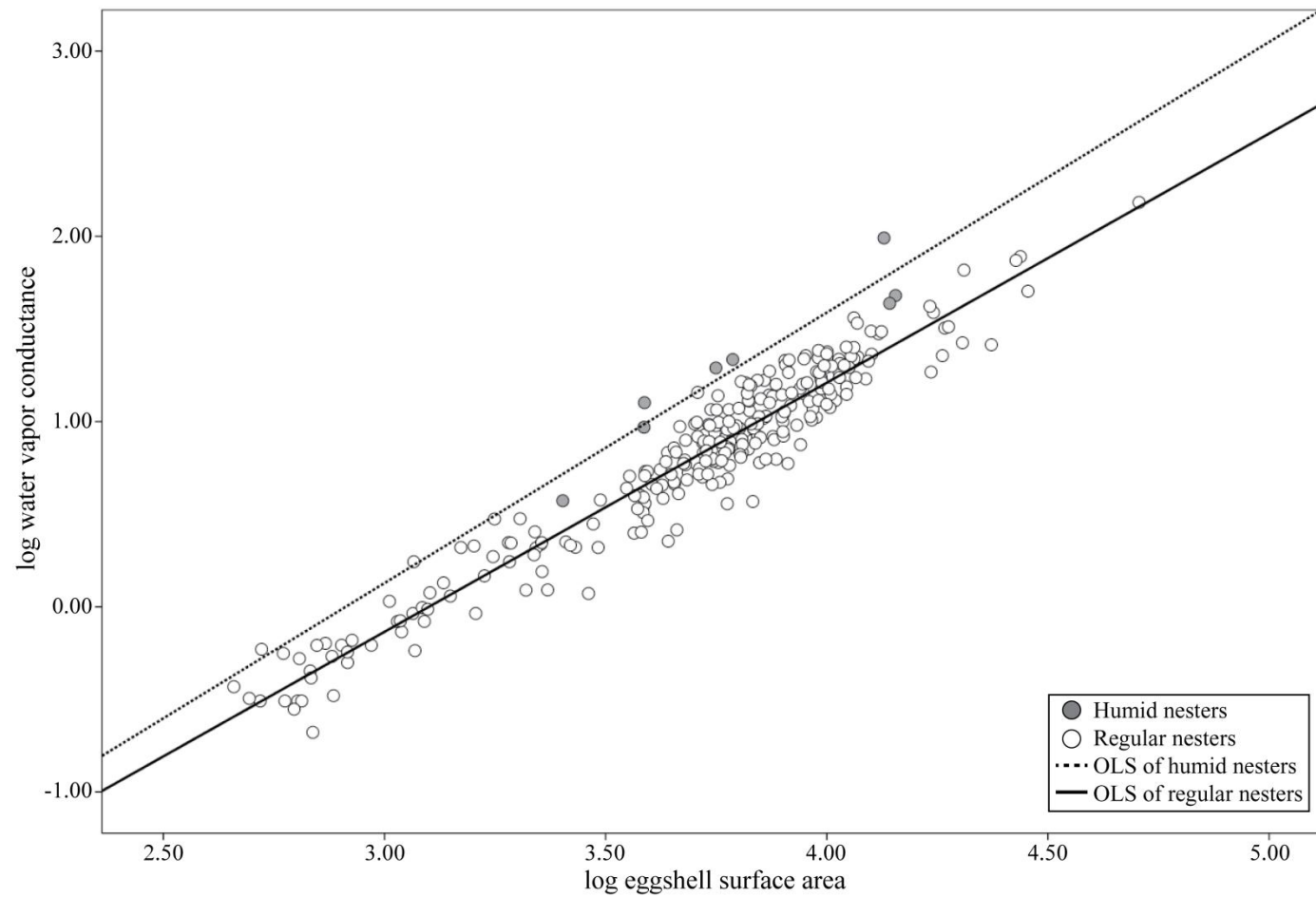


Figure 4.3: Scatter plot and OLS regressions of $\log G_{\text{H}_2\text{O}}$ and $\log V_{\text{shell}}$ between humid and regular nesters

Note that the regression of humid nesters is above that of regular nesters.

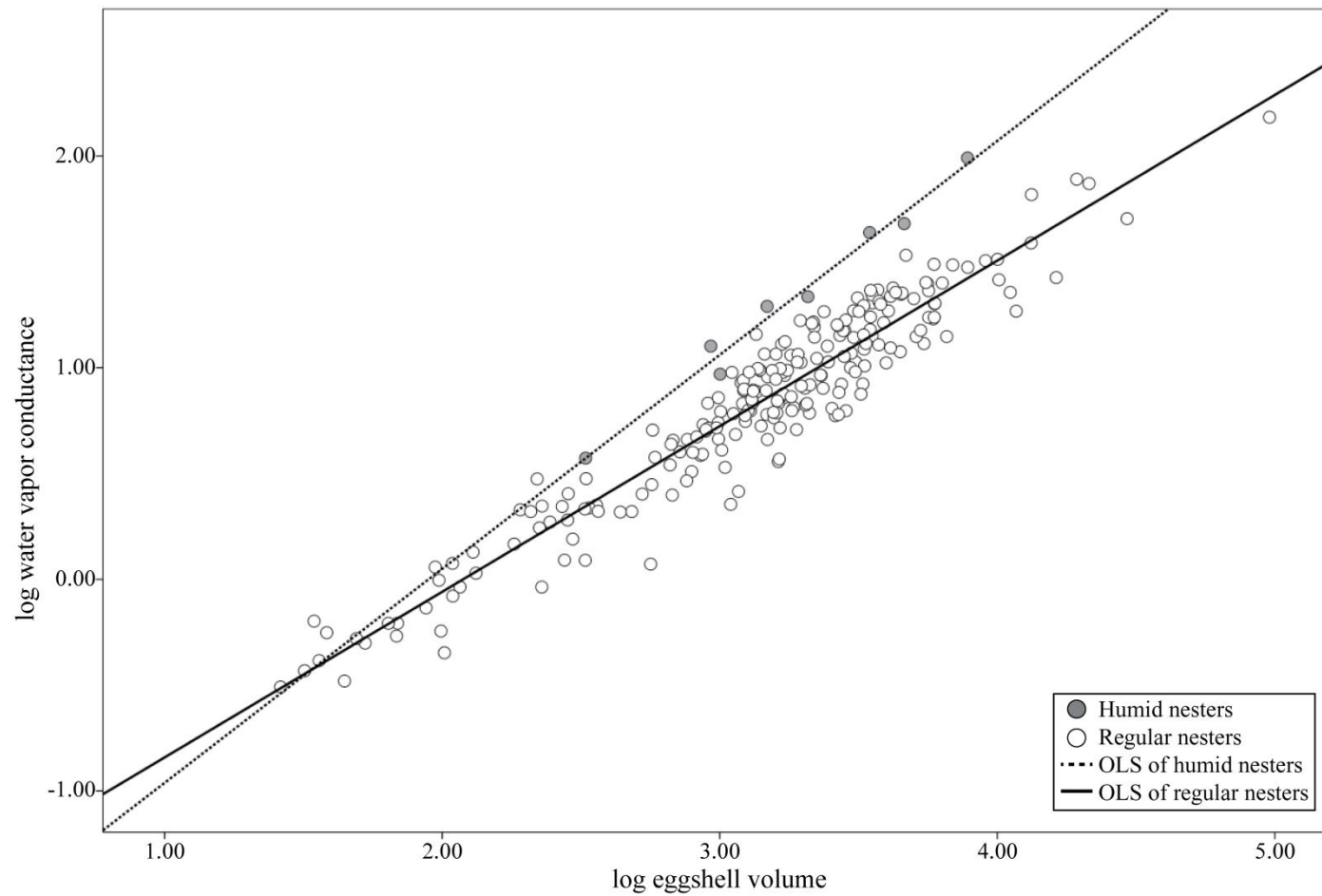


Figure 4.4: Scatter plot and OLS regressions of $\log G_{H_2O}$ and $\log M$ among birds and crocodilians

Note that G_{H_2O} values of crocodilian species tend to be high, whereas G_{H_2O} values of regular nesters that build scrape nests or lack nests in arid environments tend to be low. Shadow area indicates the 95 % confidence intervals of bird regular nesters.

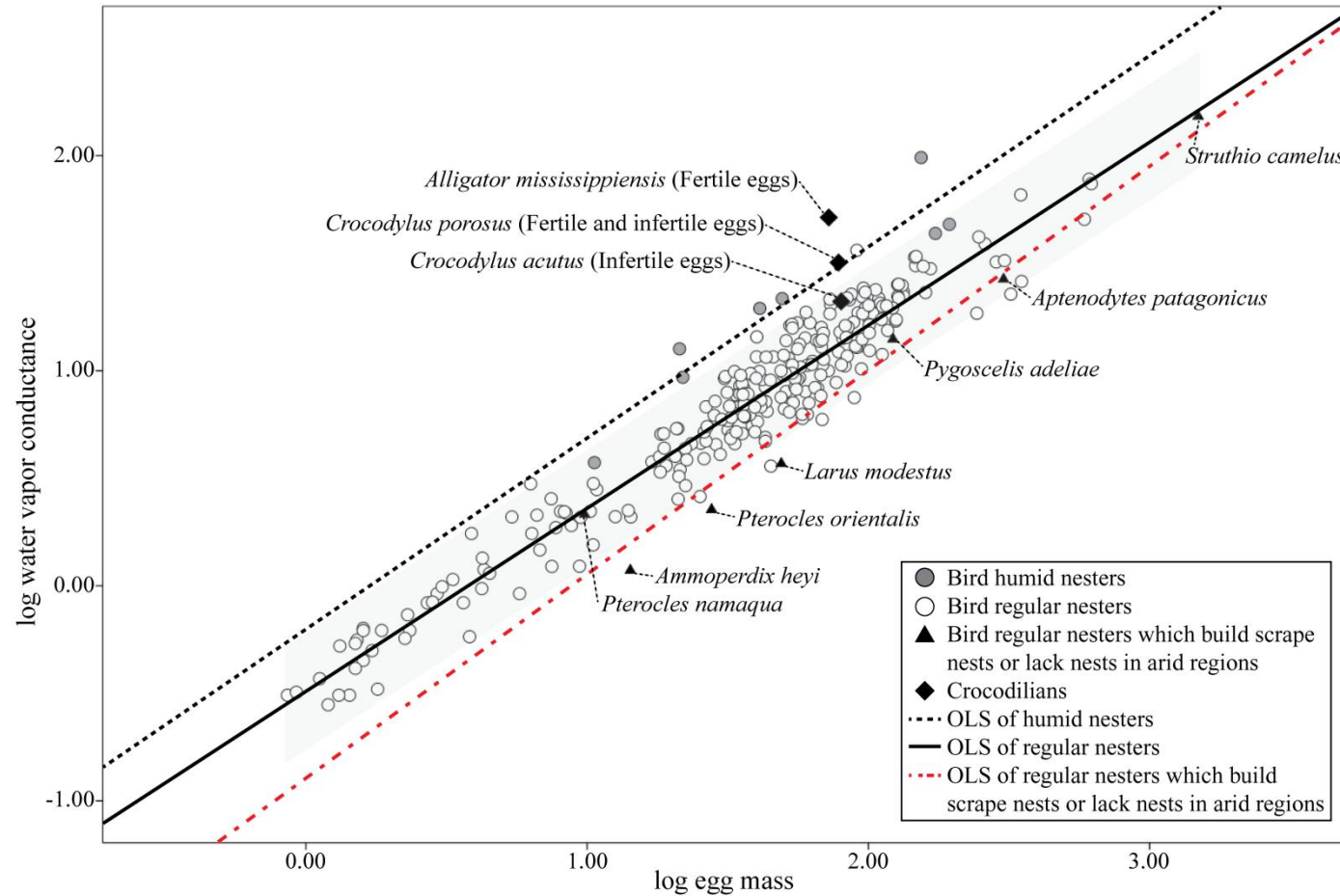


Figure 4.5: Scatter plot and OLS regressions of $\log G_{H_2O}$ and $\log A_s$ among birds and crocodilians

Note that G_{H_2O} values of crocodilian species tend to be high, whereas G_{H_2O} values of regular nesters that build scrape nests or lack nests in arid environments tend to be low. Shadow area indicates the 95 % confidence intervals of bird regular nesters.

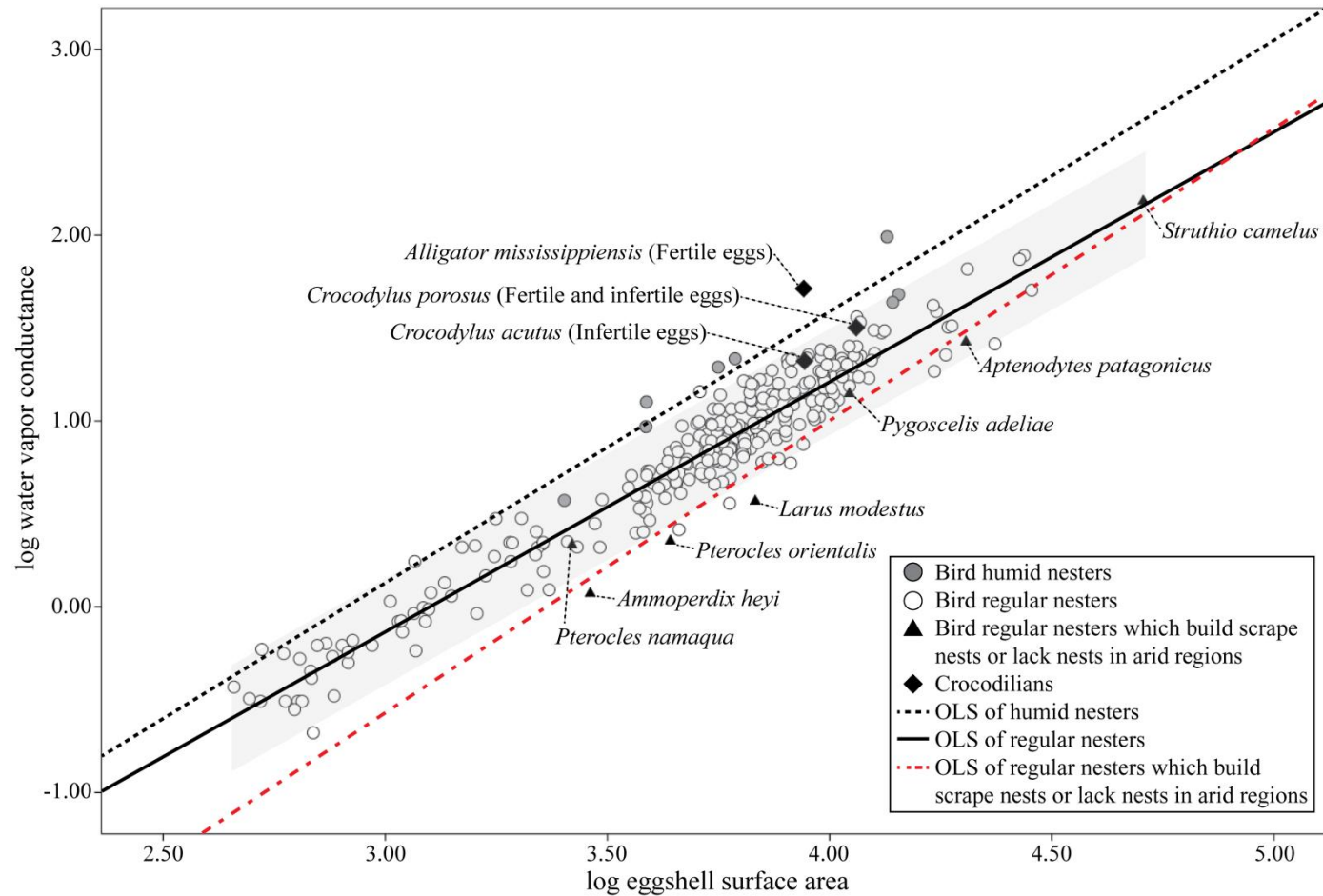
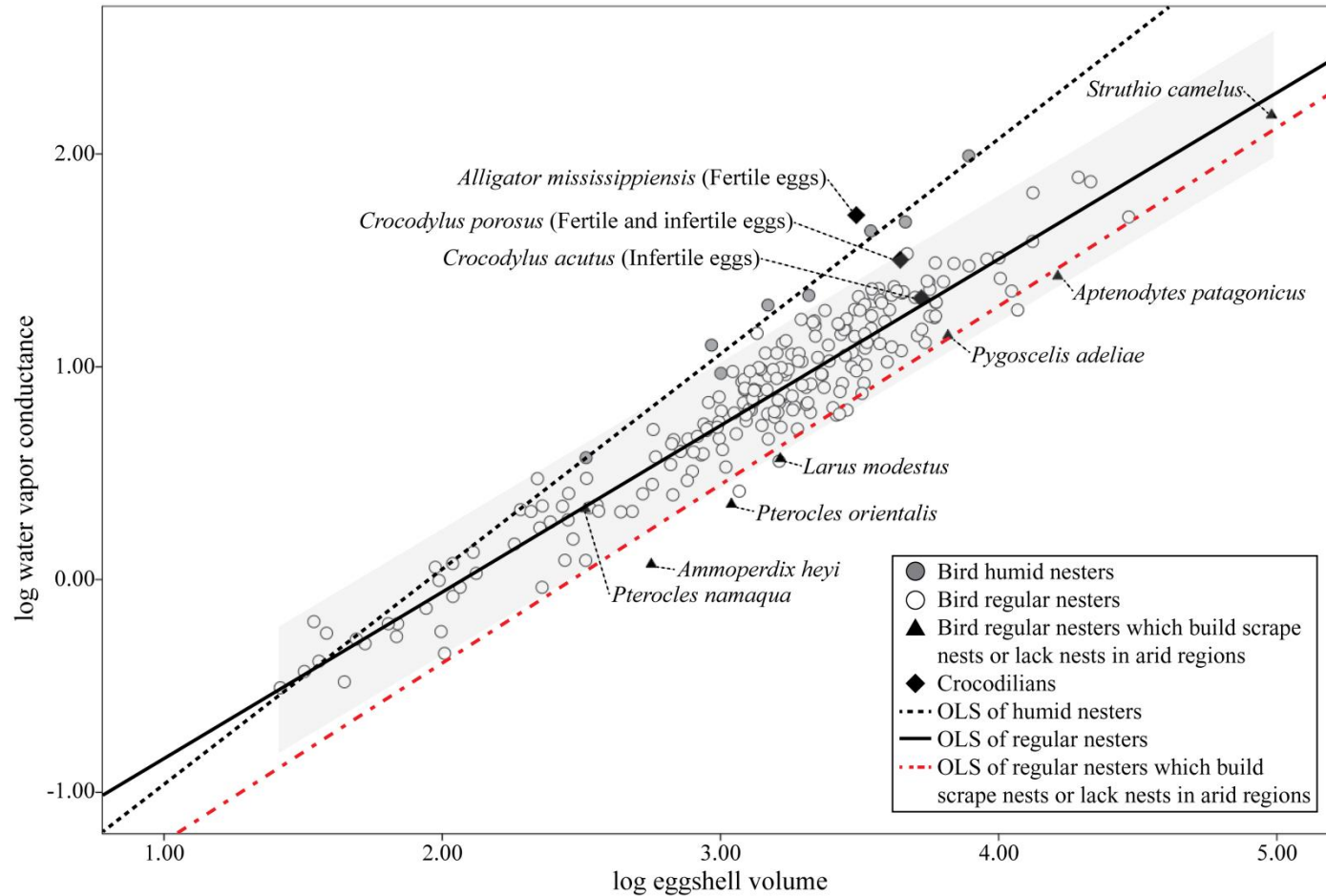


Figure 4.6: Scatter plot and OLS regressions of $\log G_{H_2O}$ and $\log V_{shell}$ among birds and crocodilians

Note that G_{H_2O} values of crocodilian species tend to be high, whereas G_{H_2O} values of regular nesters that build scrape nests or lack nests in arid environments tend to be low. Shadow area indicates the 95 % confidence intervals of bird regular nesters.



CHAPTER FIVE: CONCLUSIONS

Archosaur nests are extremely varied, in terms of architecture, location, and nesting habitat (e.g., covered nests, non-covered scrape nests, and non-covered cup nests), and thus have varying nest microclimates. Incubation temperature tends to be relatively consistent among species of birds and crocodilians, regulated by nesting and brooding behaviors. Nest humidity varies significantly among archosaur species, unlike temperature, and has a direct effect on the water vapor conductance of the eggs. This study examined for relationships between nest environment (i.e., nest type, nest humidity) and water vapor conductance (G_{H_2O}) of the eggs in living archosaurs using statistical approaches because estimates of G_{H_2O} in the eggs of extinct archosaurs has been widely used previously to infer their nest types/modes.

This study shows that nest humidity of archosaurs appears to be related to nest architecture as well as other factors, such as wetness of the nest materials. Statistical analyses of 54 archosaur species revealed that absolute nest humidity (P_{nest}) is significantly higher for those that build covered nests (i.e., mounds and infilled holes) than those that build non-covered nest (i.e., scrape and cup), regardless of the ambient humidity of nesting habitats. The gradient between nest humidity and ambient humidity (ΔP) is also higher in species with covered nests (i.e., megapodes and crocodilians) than species with non-covered nests. Presumably the differences in P_{nest} and ΔP between covered and non-covered nests are because covered nests retain more humidity. Some species that build non-covered highly aquatic nests also appear to have a high nest humidity (e.g., grebes, black terns), which is likely due to the behavior of building floating nests that usually result in a wet nest cup. In other species, such as for the ostrich, extremely low nest humidity appears to be a combination of scrape nest style (no or little nest material) and an arid climate. While nest architecture appears to have a strong influence on nest humidity, it is apparent that in some taxa other factors or behaviors can also affect nest humidity.

This study also reveals that the water vapor conductance of the eggs is related to the type of the nesters among birds. Comparisons between 285 taxa of humid and regular nester types compiled from the literature show that water vapor conductance is strongly correlated with egg sizes (i.e., egg mass, eggshell surface area, and eggshell volume)

among birds and that G_{H_2O} is significantly higher in humid nesters than in regular nesters. These results show that G_{H_2O} is an indicator of nester types among birds, which potentially could be used for prediction of nester types among extinct archosaurs such as dinosaurs. While estimates of G_{H_2O} for dinosaur eggs have been used previously to infer their nest types/modes, it was unknown, until now, if there was a correlation between G_{H_2O} and nest types among living birds. While this study shows that there is a correlation between G_{H_2O} and nest types in living birds, the methods used for the estimation of G_{H_2O} in extinct taxa is still questionable.

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APPENDIX A: MEAN RAW VALUES OF G_{H_2O} AND EGG SIZES (CHAPTER FOUR)

G_{H_2O} represents average water vapour conductance of egg, M is average egg mass, L is average maximum egg length, B is average maximum egg breadth, and L_s is average shell thickness (= pore length). Schonwetter (1960-1967) was only used for L and B.

<i>Species</i>	G_{H_2O} (mgH ₂ O/day/Torr)	M (g)	L (mm)	B (mm)	L_s (mm)	Sources
Accipitridae						
<i>Aquila rapax</i>	13.00	92.80	68.70	53.68	0.520	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Buteo rufinus</i>	6.26	60.72	57.98	45.80	0.371	Schonwetter (1960-1967); Ar and Rahn (1985)
<i>Gyps fulvus</i>	18.50	243.00	91.20	69.50	0.680	Schonwetter (1960-1967); Ar and Rahn (1978)
Anseriformes						
<i>Aix galericulata</i>	5.58	38.63	48.80	36.30	0.240	Harrison (1975); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Aix sponsa</i>	6.48	43.62	51.20	38.80	0.320	Schonwetter (1960-1967); Ar and Rahn

						(1978, 1985); Hoyt et al. (1979); French and Board (1983)
<i>Anas acuta</i>	3.60	45.00	54.70	38.20	0.273	Schonwetter (1960-1967); French and Board (1983)
<i>Anas americana</i>	7.20	43.00	54.30	38.50		Schonwetter (1960-1967); French and Board (1983)
<i>Anas bahamensis</i>	8.50	34.90	52.45	35.50	0.225	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); Ar and Rahn (1985)
<i>Anas capensis</i>	9.20	30.80	56.00	39.80	0.270	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Anas carolinensis</i>	2.60	25.20	45.80	34.20	0.255	Schonwetter (1960-1967); French and Board (1983); Rohwer (1988)
<i>Anas castanea</i>	11.60	40.00	51.30	37.00	0.265	Schonwetter (1960-1967); French and Board (1983)
<i>Anas chlorotis</i>	16.70	62.00	60.00	42.60		Schonwetter (1960-1967); French and Board (1983)
<i>Anas discors</i>	4.60	25.40	46.60	33.40	0.219	Schonwetter (1960-1967); Hoyt et al. (1979)
<i>Anas erythrorhyncha</i>	9.65	38.45	49.70	37.40	0.260	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)

<i>Anas falcata</i>	7.20	41.30	56.00	39.40	0.270	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Anas flavirostris</i>	6.00	28.70	53.20	37.35	0.260	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Anas fulvigula</i>	16.70	55.90	57.20	42.50	0.280	Schonwetter (1960-1967); Hoyt et al. (1979)
<i>Anas gracilis</i>	7.70	33.85	49.30	36.60	0.260	Serventy and Whittell (1962); Hoyt et al. (1979); French and Board (1983)
<i>Anas luzonica</i>	13.80	51.00	50.70	38.50		Temme (1976); French and Board (1983)
<i>Anas melleri</i>	16.20	52.60	52.70	42.50		Schonwetter (1960-1967); French and Board (1983); Kear (2005)
<i>Anas penelope</i>	5.80	40.35	54.50	38.70	0.260	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)
<i>Anas platalea</i>	7.80	34.90	54.00	39.00	0.202	Schonwetter (1960-1967); Tyler (1963); Hoyt et al. (1979)
<i>Anas platyrhynchos</i>	15.58	83.75	57.75	41.05	0.325	Ar et al. (1974); Ar and Rahn (1978, 1985); Burton and Tullet (1983); Mand et al. (1986); Rokitka and Rahn (1987)
<i>Anas p. diazi</i>	11.45	52.00	56.80	41.20	0.270	Bellrose (1976); Tullett (1976); Hoyt et al. (1979); French and Board (1983)

<i>Anas p. platyrhynchos</i>	12.90	68.15	56.80	41.20	0.250	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983)
<i>Anas puna</i>	7.17	43.15	55.90	38.00	0.270	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Carey et al. (1989b)
<i>Anas poecilorhyncha poecilorhyncha</i>	9.30	57.00	56.00	42.30		Schonwetter (1960-1967); French and Board (1983)
<i>Anas p. zonorhyncha</i>	13.00		55.50	41.60		Schonwetter (1960-1967); French and Board (1983)
<i>Anas rhynchotis rhynchotis</i>	4.90	43.00	55.30	38.00		Schonwetter (1960-1967); French and Board (1983)
<i>Anas sibilatrix</i>	7.90	53.00	58.40	41.00		Schonwetter (1960-1967); French and Board (1983)
<i>Anas smithii</i>	7.30	36.20	53.30	38.70	0.280	McLachlan and Liversidge (1970); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Anas sparsa sparsa</i>	10.00	72.00	62.50	45.10		Schonwetter (1960-1967); French and Board (1983)
<i>Anas versicolor</i>	5.30	31.70	49.00	34.40	0.290	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983)
<i>Anas wyvilliana</i>	9.50	50.00	58.28	38.26	0.270	Hoyt et al. (1979); Engilis et al. (2002)

<i>Anser albifrons flavirostris</i>	15.40	117.00	80.00	52.00		Ogilvie (1978); French and Board (1983)
<i>Anser a. frontalis</i>	23.30	133.00	80.10	53.50	0.323	French and Board (1983); Ely and Raveling (1984)
<i>Anser a. gambelli</i>	22.30	133.00	82.00	53.90		Schonwetter (1960-1967); French and Board (1983)
<i>Anser anser</i>	29.80	166.27	85.75	57.60	0.598	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985); Hoyt et al. (1979); Vleck et al. (1979); Mand et al. (1986)
<i>Anser brachyrhynchus</i>	24.90	131.80	78.90	52.80	0.501	Schonwetter (1960-1967); Hoyt et al. (1979); Rahn et al. (1983); Ar and Rahn (1985)
<i>Anser cygnoides</i>	30.80	147.20	83.80	56.40	0.470	Schonwetter (1960-1967); Hoyt et al. (1979); Ar and Rahn (1985)
<i>Anser erythropus</i>	22.20	127.30	76.00	49.00	0.450	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Anser fabalis</i>	23.10	159.65	84.05	56.45	0.448	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); Ar and Rahn (1985)

<i>Anser f. rossicus</i>	33.70	146.00				French and Board (1983)
<i>Anser indicus</i>	17.00	124.90	84.00	55.10	0.480	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); Snyder et al. (1982)
<i>Aythya affinis</i>	8.00	51.00	57.10	39.70	0.316	Schonwetter (1960-1967); French and Board (1983)
<i>Aythya americana</i>	13.90	65.30	60.20	43.40	0.410	Low (1945); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Aythya baeri</i>	4.70	43.00	52.00	38.20		Schonwetter (1960-1967); French and Board (1983)
<i>Aythya fuligula</i>	9.10	56.00	59.00	41.00		Schonwetter (1960-1967); French and Board (1983)
<i>Aythya marila mariloides</i>	13.70	67.00	63.50	42.70		Schonwetter (1960-1967); French and Board (1983)
<i>Aythya novaeseelandiae</i>	11.07	63.23	65.07	44.20	0.280	Oliver (1955); Tullett (1976); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Aythya nyroca</i>	8.40	43.00	52.50	38.20		Schonwetter (1960-1967); French and Board (1983)
<i>Aythya valisineria</i>	15.90	68.00	62.40	43.80		Schonwetter (1960-1967); French and Board (1983)

<i>Biziura lobata</i>	21.80	128.00	80.40	53.50		Schonwetter (1960-1967); French and Board (1983)
<i>Branta canadensis</i>	30.60	156.80	86.00	58.20	0.520	Schonwetter (1960-1967); Tullett (1976); Snyder et al. (1982); Ar and Rahn (1985)
<i>Branta c. parvipes</i>	36.30	91.00	79.70	53.74		French and Board (1983); Ely et al. (2008)
<i>Branta hutchinsii leucopareia</i>	22.50	104.90	77.00	54.00	0.400	Stephenson and Smart (1972); Tullett (1976); Hoyt et al. (1979); French and Board (1983)
<i>Branta h. minima</i>	17.35	100.70	73.66	48.58	0.360	Schonwetter (1960-1967); Manning (1978); Hoyt et al. (1979); Ar and Rahn (1985)
<i>Branta leucopsis</i>	21.70	108.90	79.35	50.50	0.388	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983); Rahn et al. (1983); Ar and Rahn (1985)
<i>Branta ruficollis</i>	10.53	82.60	70.60	48.70	0.420	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Branta sandvicensis</i>	33.97	147.80	78.20	55.00	0.400	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Bucephala albeola</i>	5.10	35.60	50.50	36.10	0.360	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)

<i>Bucephala clangula</i>	10.60	60.60	59.45	43.00	0.270	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983)
<i>Bucephala islandica</i>	10.63	68.73	62.00	45.10	0.390	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Cairina moschata</i>	12.23	78.35	64.00	46.00	0.400	Schonwetter (1960-1967); Ar et al. (1974); French and Board (1983); Ar and Rahn (1978, 1985)
<i>Cairina scutulata</i>	21.35	85.55	62.50	45.50	0.390	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)
<i>Callonetta leucophrys</i>	5.85	31.80	46.50	35.20		Hoyt et al. (1979); French and Board (1983); Kear (2005)
<i>Cereopsis novaehollandiae</i>	17.27	125.65	78.85	54.45	0.487	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1985); Wagner and Seymour (2001)
<i>Chen caerulescens atlantica</i>	25.10	127.00	80.70	53.40	0.550	Schonwetter (1960-1967); French and Board (1983)
<i>Chen canagica</i>	25.25	128.05	79.10	52.20	0.500	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)

<i>Chen rossii</i>	18.60	91.90	73.60	47.70	0.320	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)
<i>Chenonetta jubata</i>	7.10	54.00	56.80	41.00		Schonwetter (1960-1967); French and Board (1983)
<i>Chloephaga melanoptera</i>	11.89	111.94	74.70	50.10	0.440	Carey et al. (1990)
<i>Chloephaga picta leucoptera</i>	23.80	106.10	75.40	49.30	0.420	Goodall et al. (1946-1951); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Chloephaga p. picta</i>	19.60	122.00	79.80	52.60		Schonwetter (1960-1967); French and Board (1983)
<i>Chloephaga poliocephala</i>	10.20	94.50	70.40	47.80	0.360	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)
<i>Chloephaga rubidiceps</i>	11.70	84.10	69.50	48.40	0.320	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Clangula hyemalis</i>	11.60	45.90	53.90	38.85	0.266	Schonwetter (1960-1967); Rahn et al. (1983); Ar and Rahn (1985)
<i>Cyanochen cyanoptera</i>	15.03	83.60	70.00	50.00	0.290	Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985); Kear (2005)
<i>Cygnus columbianus bewickii</i>	38.80	260.00	103.00	67.00	0.760	Schonwetter (1960-1967); French and Board (1983)

<i>Cygnus melanocoryphus</i>	41.90	247.00	101.00	66.50		Schonwetter (1960-1967); French and Board (1983)
<i>Cygnus olor</i>	65.70	348.20	112.50	73.50	0.650	Schonwetter (1960-1967); Booth (1989); Booth and Sotherland (1991)
<i>Dendrocygna arborea</i>	14.20	59.60	54.30	42.00	0.410	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Dendrocygna arcuata</i>	6.10	36.50	51.30	37.40	0.380	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Dendrocygna autumnalis</i>	11.57	43.27	51.40	37.90	0.340	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Dendrocygna bicolor</i>	16.43	53.47	53.10	41.45	0.340	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Dendrocygna guttata</i>	11.80	50.00	53.50	40.80		Schonwetter (1960-1967); French and Board (1983)
<i>Dendrocygna viduata</i>	8.30	36.00	47.80	36.50		Schonwetter (1960-1967); French and Board (1983)
<i>Heteronetta atricapilla</i>	18.70	60.00	59.20	43.90		Schonwetter (1960-1967); French and Board (1983)

<i>Lophodytes cucullatus</i>	8.38	54.88	53.60	44.30	0.470	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Marmaronetta angustirostris</i>	9.40	31.00	46.30	34.40		Schonwetter (1960-1967); French and Board (1983)
<i>Merganetta armata armata</i>	10.40	57.33	63.00	41.17		French and Board (1983); Eldridge (1986)
<i>Mergellus albellus</i>	9.10	42.00	52.70	37.50		Schonwetter (1960-1967); French and Board (1983)
<i>Mergus merganser merganser</i>	14.95	69.15	67.50	46.50	0.320	Schonwetter (1960-1967); Hoyt et al. (1979); Ar and Rahn (1985)
<i>Mergus serrator</i>	5.93	68.50	64.90	45.10	0.320	Schonwetter (1960-1967); Tullett (1976); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Neochen jubata</i>	10.70	63.00	60.20	42.80		Schonwetter (1960-1967); French and Board (1983)
<i>Netta peposaca</i>	15.80	53.70	55.00	42.00	0.400	Delacour (1959); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Netta rufina</i>	9.20	54.85	57.80	41.50	0.340	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)

<i>Oxyura jamaicensis</i>	20.23	73.47	62.30	45.70	0.440	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Oxyura leucocephala</i>	22.07	95.20	66.70	50.70	0.370	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Oxyura maccoa</i>	24.20	96.00	67.20	50.50		Schonwetter (1960-1967); French and Board (1983)
<i>Oxyura vittata</i>	22.70	87.00	65.50	48.50	0.480	Schonwetter (1960-1967); Hoyt et al. (1979); Mallory and Weatherhead (1990)
<i>Sarkidiornis melanotos melanotos</i>	8.30	66.00	61.60	43.50	0.280	Schonwetter (1960-1967); French and Board (1983)
<i>Somateria fischeri</i>	18.40	73.00	66.20	44.70	0.290	Schonwetter (1960-1967); French and Board (1983)
<i>Somateria mollissima</i>	18.53	103.67	78.00	51.02	0.380	Ar and Rahn (1978, 1985); Rahn et al. (1983); Mand et al. (1986)
<i>Somateria m. mollissima</i>	20.60	110.05	77.00	51.50	0.350	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)
<i>Somateria spectabilis</i>	21.50	73.00	67.00	44.50		Schonwetter (1960-1967); French and Board (1983)

<i>Tadorna ferruginea</i>	14.15	81.05	68.00	47.00	0.400	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Mallory and Weatherhead (1990)
<i>Tadorna tadorna</i>	15.13	79.30	65.60	47.30	0.400	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Tadorna variegata</i>	12.83	90.87	67.40	48.40	0.410	Schonwetter (1960-1967); Hoyt et al. (1979); French and Board (1983); Ar and Rahn (1985)
<i>Thalassornis leuconotus leuconotus</i>	21.80	84.00	63.70	48.90		Schonwetter (1960-1967); French and Board (1983)
Caprimulgiformes						
<i>Chordeiles acutipennis</i>	0.92	5.75	27.04	19.73	0.142	Schonwetter (1960-1967); Grant (1982)
Cathartidae						
<i>Vultur gryphus</i>	22.70	321.00	110.00	68.00	0.610	Schonwetter (1960-1967); Ar and Rahn (1985)
Charadriiformes						
<i>Anous minutus marculsi</i>	4.58	23.47	44.70	31.00	0.190	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985); Whittow (1980)

<i>Anous stolidus pileatus</i>	6.25	37.90	52.75	36.45	0.235	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985)
<i>Burhinus oedicephalus</i>	4.58	33.50	50.90	37.40	0.270	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Charadrius alexandrinus</i>	1.23	7.49	31.30	22.35	0.157	Schonwetter (1960-1967); Grant (1982)
<i>Charadrius vociferus</i>	2.09	14.30	38.15	27.05	0.159	Schonwetter (1960-1967); Ar and Rahn (1978); Grant (1982)
<i>Chlidonias leucopterus</i>	2.24	14.00	34.60	25.00	0.140	Schonwetter (1960-1967); Ar and Rahn (1985)
<i>Chlidonias niger</i>	3.74	10.61	34.60	24.63	0.130	Schonwetter (1960-1967); Ar and Rahn (1985); Davis and Ackerman (1985)
<i>Fratercula arctica</i>	7.99	59.68	62.10	43.53	0.310	Schonwetter (1960-1967); Ar et al. (1974); Ar and Rahn (1978, 1985)
<i>Fratercula cirrhata</i>	13.00	89.90	71.00	49.00	0.351	Tullett (1976); Ar and Rahn (1978, 1985); Zimmermann and Hipfner (2007)
<i>Gelochelidon nilotica</i>	6.20	28.31	48.02	34.32	0.211	Schonwetter (1960-1967); Grant et al. (1984); Ar and Rahn (1985)
<i>Glareola pratincola</i>	2.18	8.43	31.70	23.75	0.150	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Gygis alba</i>	3.47	21.40	41.61	31.37	0.172	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985); Pettit et

						al. (1981)
<i>Haematopus ostralegus</i>	6.80	41.48	57.56	39.56	0.253	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Himantopus mexicanus</i>	5.38	21.00	43.80	30.50	0.224	Grant (1982)
<i>Larus argentatus</i>	16.81	88.49	71.06	49.57	0.293	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985); Morgan et al. (1978)
<i>Larus atricilla</i>	9.05	44.80	54.00	38.50	0.250	Schonwetter (1960-1967); Vleck et al. (1983); Ar and Rahn (1985)
<i>Larus canus</i>	13.27	56.94	59.67	42.01	0.243	Schonwetter (1960-1967); Ar et al. (1974); Lomholt (1976); Tullett (1976); Ar and Rahn (1978, 1985); Vleck et al. (1983); Mand et al. (1986)
<i>Larus fuscus</i>	15.94	84.60	67.50	47.05	0.300	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Larus glaucescens</i>	23.19	97.40	73.05	50.00	0.350	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Morgan et al. (1978)
<i>Larus heermanni</i>	10.63	53.60	58.75	42.10	0.271	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Rahn and Dawson (1979)
<i>Larus livens</i>	19.65	97.70	72.50	50.10	0.331	Ar and Rahn (1978, 1985); Rahn and Dawson (1979)

<i>Larus marinus</i>	19.95	112.27	73.54	50.92	0.370	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Larus modestus</i>	3.70	49.00	58.20	41.20	0.241	Schonwetter (1960-1967); Guerra et al. (1988); Monge et al. (2000)
<i>Larus ridibundus</i>	8.71	35.56	52.60	37.00	0.218	Schonwetter (1960-1967); Lomholt (1976); Ar and Rahn (1978, 1985)
<i>Larus serranus</i>	8.20	55.40	60.75	41.50	0.278	Schonwetter (1960-1967); Carey et al. (1987)
<i>Limosa limosa</i>	9.50	39.09	53.45	36.85	0.197	Schonwetter (1960-1967); Visser et al. (1995); Tanaka pers. obs.
<i>Numenius arquata</i>	16.21	82.77	68.20	47.65	0.238	Schonwetter (1960-1967); Visser et al. (1995); Tanaka pers. obs.
<i>Numenius phaeopus</i>	9.74	53.50	59.48	41.53	0.200	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Onychoprion fuscatus</i>	6.77	34.53	51.11	35.83	0.230	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985)
<i>Onychoprion lunatus</i>	4.54	28.69	45.30	32.20	0.160	Schonwetter (1960-1967); Whittow et al. (1985)
<i>Philomachus pugnax</i>	3.62	19.10	43.50	30.60		Schonwetter (1960-1967); Visser et al. (1995)

<i>Pluvialis apricaria</i>	5.01	32.61	52.05	35.25	0.170	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Pluvianus aegyptius</i>	2.08	9.48	30.90	23.70	0.199	Howell (1979)
<i>Ptychoramphus aleuticus</i>	4.08	29.74	46.90	33.90	0.220	Roudybush et al. (1980); Ar and Rahn (1985); Hipfner et al. (2004); Zimmermann and Hipfner (2007)
<i>Recurvirostra americana</i>	4.84	32.40	50.30	33.60	0.236	Grant (1982)
<i>Rissa tridactyla</i>	9.71	50.68	57.05	41.38	0.260	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Morgan et al. (1978)
<i>Rynchops niger</i>	6.80	26.45	44.93	33.22	0.208	Schonwetter (1960-1967); Grant et al. (1984); Ar and Rahn (1985)
<i>Stercorarius maccormicki</i>	16.30	100.65	71.30	49.60	0.400	Ar and Rahn (1978, 1985); Hemmings (1984)
<i>Stercorarius skua</i>	18.41	95.49	70.45	49.35	0.330	Schonwetter (1960-1967); Ar et al. (1974); Harrison (1975); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Sterna forsteri</i>	3.23	21.20	42.80	30.70	0.206	Schonwetter (1960-1967); Grant (1982)
<i>Sterna hirundo</i>	4.00	20.57	42.06	30.64	0.190	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985); Mand et al. (1986)

<i>Sterna paradisaea</i>	5.07	18.30	41.05	29.70	0.160	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985)
<i>Sternula albifrons</i>	1.91	8.79	31.67	23.01	0.130	Schonwetter (1960-1967); Rahn et al. (1976); Ar and Rahn (1978, 1985)
<i>Thalasseus elegans</i>	9.92	40.95	53.00	37.50	0.290	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Thalasseus maximus</i>	13.93	68.47	63.50	44.50	0.277	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Vleck et al. (1983); Rokitka and Rahn (1987)
<i>Thalasseus sandvicensis</i>	7.84	36.40	51.25	35.85	0.250	Schonwetter (1960-1967); Lomholt (1976); Vleck et al. (1983); Ar and Rahn (1985)
<i>Tringa totanus</i>	4.35	22.35	45.03	31.53	0.162	Schonwetter (1960-1967); Visser et al. (1995); Tanaka pers. obs.
<i>Uria aalge</i>	20.05	116.00	83.96	46.18	0.603	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1978; 1985); Zimmermann and Hipfner (2007)
<i>Uria lomvia</i>	17.30	111.30	79.58	50.58	0.555	Schonwetter (1960-1967); Rahn et al. (1984)
<i>Vanellus vanellus</i>	4.71	26.46	46.50	33.40	0.183	Schonwetter (1960-1967); Visser et al. (1995); Tanaka pers. obs.
Ciconiiformes						

<i>Ardea albus</i>	7.52	48.90	56.23	40.18	0.263	Schonwetter (1960-1967); Vleck et al. (1983); Ar and Rahn (1985); Rokitka and Rahn (1987)
<i>Bubulcus ibis</i>	5.19	26.10	45.10	33.65	0.205	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Vleck et al. (1983)
<i>Egretta caerulea</i>	5.50	26.70	43.40	32.90	0.235	Schonwetter (1960-1967); Ar and Rahn (1985)
<i>Egretta garzetta</i>	7.21	28.50	46.20	33.55	0.219	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Egretta thula</i>	3.85	22.60	44.00	33.00	0.200	Schonwetter (1960-1967); Vleck et al. (1983); Ar and Rahn (1985)
<i>Egretta tricolor</i>	3.90	26.05	42.17	31.07	0.225	Schonwetter (1960-1967); Vleck et al. (1983); Ar and Rahn (1985)
<i>Eudocimus albus</i>	6.65	50.25	58.00	39.00	0.320	Baicich and Harrison (1997); Vleck et al. (1983); Ar and Rahn (1985)
<i>Nycticorax nycticorax</i>	6.30	33.70	51.77	37.03	0.230	Schonwetter (1960-1967); Vleck et al. (1983); Ar and Rahn (1978, 1985)
<i>Plegadis falcinellus</i>	7.80	37.30	52.15	36.30	0.271	Schonwetter (1960-1967); Vleck et al. (1983); Ar and Rahn (1985)
<i>Plegadis ridgwayi</i>	5.20	33.90	52.00	34.70	0.321	Schonwetter (1960-1967); Carey et al. (1987)

Columbiformes						
<i>Columba livia</i>	3.77	17.01	37.49	27.69	0.190	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1978); Vleck et al. (1979); Arad et al. (1988)
<i>Streptopelia decaocto</i>	2.54	7.45	30.30	23.93	0.130	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Streptopelia roseogrisea</i>	2.22	8.04	28.65	22.05	0.120	Ar and Rahn (1978, 1985); Hubbard (2005)
<i>Streptopelia senegalensis</i>	2.13	6.63	25.95	20.23	0.120	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Ponomareva (1981)
<i>Streptopelia turtur</i>	2.21	8.30	29.10	22.03	0.140	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Zenaida macroura</i>	1.87	7.73	28.13	20.77	0.139	Schonwetter (1960-1967); Kreitzer (1971); Walsberg (1985)
Coraciiformes						
<i>Merops ornatus</i>	1.19	4.30	21.68	18.98	0.086	Lill and Fell (2007)
Falconidae						
<i>Falco naumanni</i>	2.80	10.82	34.90	28.25	0.192	Schonwetter (1960-1967); Ar and Rahn (1978; 1985)
<i>Falco tinnunculus</i>	3.98	18.10	39.02	31.55	0.218	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1978)

Galliformes						
<i>Alectoris graeca</i>	3.38	18.20	41.68	30.49	0.280	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Alectura lathamii</i>	47.94	194.00	92.50	59.83	0.323	Schonwetter (1960-1967); Seymour and Rahn (1978); Vleck et al. (1984); Ar and Rahn (1985); Seymour et al. (1986); Booth and Thompson (1991)
<i>Ammoperdix heyi</i>	1.18	14.24	36.00	27.00	0.195	Schonwetter (1960-1967); Ar and Rahn (1985)
<i>Bonasa umbellus togata</i>	4.37	18.79	39.20	30.30		Schonwetter (1960-1967); Bendell and Bendell-Young (2006)
<i>Chrysolophus amherstiae</i>	5.95	30.08	46.30	35.00	0.260	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Chrysolophus pictus</i>	6.07	32.60	43.70	33.60	0.259	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Coturnix coturnix</i>	2.99	10.53	29.32	22.88	0.163	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985); Vleck et al. (1979)
<i>Falciennis canadensis canace</i>	5.38	20.79	43.20	31.10		Schonwetter (1960-1967); Bendell and Bendell-Young (2006)

<i>Gallus gallus</i>	12.64	56.02	58.75	44.13	0.329	Ar et al. (1974); Tullett (1976, 1981); Rahn et al. (1977b); Ar and Rahn (1978, 1985); Arad and Marder (1981); Tullett and Deeming (1982); Burton and Tullett (1983); Leon-Velarde et al. (1984a); Visschedijk et al. (1985); Andersen and Steen (1986); Rokitka and Rahn (1987); Seymour and Visschedijk (1988); Booth and Rahn (1989); O'dea et al. (2004); Narushin (2005); Hamidu et al. (2007)
<i>Gallus g. bankiva</i>	9.70	38.10	48.00	35.90	0.308	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Lagopus lagopus</i>	2.92	22.40	42.70	31.43	0.193	Schonwetter (1960-1967); Carey and Martin (1997)
<i>Lagopus leucura</i>	2.50		42.55	29.55	0.184	Schonwetter (1960-1967); Carey and Martin (1997)
<i>Leipoa ocellata</i>	43.50	173.00	91.30	58.70	0.250	Schonwetter (1960-1967); Vleck et al. (1984); Seymour et al. (1986, 1987); Booth and Seymour (1987)
<i>Lophophorus impejanus</i>	8.35	64.56	63.70	44.70	0.344	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1978, 1985)

<i>Lophura nycthemera</i>	9.24	39.91	52.20	40.50	0.375	Schonwetter (1960-1967); Ar et al. (1974); Ar and Rahn (1978, 1985)
<i>Lophura swinhoii</i>	7.30	41.38	52.20	38.60	0.311	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Meleagris gallopavo</i>	14.29	83.39	63.75	46.32	0.396	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976, 1981); Ar and Rahn (1978, 1985); Burton and Tullett (1983); Rokitka and Rahn (1987)
<i>Numida meleagris galeatus</i>	10.00	48.90	51.27	40.13	0.493	Schonwetter (1960-1967); Tullett (1976); Ancel and Girard (1992)
<i>Pavo cristatus</i>	14.02	95.09	70.65	51.80	0.500	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Pavo muticus</i>	20.13	100.23	73.20	53.80	0.545	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Phasianus colchicus</i>	6.84	32.09	44.43	34.80	0.288	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Syrmaticus soemmerringii</i>	7.93	31.48	47.05	34.95	0.255	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
Gaviiformes						
<i>Gavia immer</i>	98.00	154.00	90.30	57.60	0.580	Schonwetter (1960-1967); Ar and Rahn (1985)

Gruiformes						
<i>Fulica americana</i>	6.96	36.16	53.03	35.45	0.302	Gullion (1954); Davis et al. (1984); Sotherland et al. (1984); Carey et al. (1989a); Brisbin et al. (2002)
<i>Fulica atra</i>	14.37	40.10	50.90	35.00	0.265	Schonwetter (1960-1967); Lomholt (1976); Tanaka pers. obs.
<i>Gallinula tenebrosa</i>	9.92	33.42	50.55	35.03	0.270	Lill (1990)
<i>Porphyrio porphyrio</i>	9.52	35.14	52.12	36.41	0.235	Lill (1990)
Passeriformes						
<i>Agelaius phoeniceus</i>	1.35	4.24	25.00	18.00	0.095	Ar et al. (1974); Rahn et al. (1977b); Ar and Rahn (1978); Carey (1979); Carey et al. (1983); Baicich and Harrison (1997)
<i>Carduelis tristis</i>	0.56	1.52	16.00	12.00	0.065	Ar and Rahn (1978); Baicich and Harrison (1997); Tanaka pers. obs.
<i>Cercotrichas galactotes</i>	0.73	2.30	22.20	16.20	0.080	Harrison (1975); Ar and Rahn (1978, 1985); Ponomareva (1981)
<i>Cinnyris osea</i>	0.31	0.86	15.50	11.00	0.050	Harrison (1975); Ar and Rahn (1978, 1985)
<i>Dendroica petechia</i>	0.45	1.60	17.00	13.00	0.150	Tullett (1976); Ar et al. (1974); Baicich and Harrison (1997)
<i>Ficedula hypoleuca</i>	0.64	1.60	17.90	13.40	0.047	Harrison (1975); Kern et al. (1992); Eeva and Lehtikoinen (1995)

<i>Galerida cristata</i>	0.92	2.93	22.70	16.80	0.100	Harrison (1975); Ar and Rahn (1978, 1985)
<i>Hippolais rama</i>	0.31		15.49	12.45		Ponomareva (1981); Hume (1889)
<i>Hirundo rustica</i>	0.33	1.80	18.90	13.30	0.058	Birchard and Kilgore (1980)
<i>Junco hyemalis</i>	0.62	2.34	20.02	15.25	0.074	Conway (1998); Nolan et al. (2002); Tanaka pers. obs.
<i>Menura novaehollandiae</i>	7.08	61.50	61.59	35.62	0.218	North (1889); Lill (1987)
<i>Molothrus ater</i>	1.07	3.33	21.00	16.00	0.129	Ar et al. (1974); Ar and Rahn (1978); Baicich and Harrison (1997); Tanaka pers. obs.
<i>Muscicapa striata</i>	0.62	1.86	18.50	14.10	0.080	Harrison (1975); Ar and Rahn (1978, 1985)
<i>Passer ammodendri</i>	0.66		19.05	14.48		Dresser (1903); Ponomareva (1981)
<i>Passer domesticus</i>	0.83	2.70	22.50	15.70	0.102	Ar et al. (1974); Harrison (1975); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Passer moabiticus</i>	0.54	1.50	18.90	13.20	0.090	Harrison (1975); Ar and Rahn (1978, 1985)
<i>Pica pica</i>	1.23	9.40	33.50	23.50	0.118	Sotherland et al. (1979); Taigen et al. (1980); Trost (1999)
<i>Ploceus capensis</i>	0.83	3.63	24.80	16.50		Roberts (1970); Brown (1994)
<i>Ploceus cucullatus</i>	0.84	2.82	23.40	15.40		Roberts (1970); Vleck et al. (1979)
<i>Prinia gracilis</i>	0.37	1.12	13.80	10.70	0.070	Harrison (1975); Ar and Rahn (1978, 1985)
<i>Pycnonotus capensis</i>	0.99	3.05	23.80	16.90	0.080	Roberts (1970); Ar and Rahn (1978, 1985)

<i>Quiscalus quiscula</i>	2.98	6.30	28.00	21.00	0.124	Ar et al. (1974); Tullett (1976); Ar and Rahn (1978); Baicich and Harrison (1997)
<i>Riparia riparia</i>	0.41	1.50	17.70	12.60	0.053	Birchard and Kilgore (1980)
<i>Scotocerca inquieta</i>	0.59		15.75	10.92		Ponomareva (1981); Hume (1889)
<i>Serinus canaria</i>	0.62	1.60	17.20	13.30		Harrison (1975); Kern (1986); Tanvez et al. (2004)
<i>Sylvia curruca</i>	0.31	1.43	17.25	12.05		Harrison (1975); Ponomareva (1981); Payevsky (1999)
<i>Sylvia mystacea</i>	0.21		17.10	13.10		Harrison (1975); Ponomareva (1981)
<i>Tachycineta bicolor</i>	0.50	1.72	19.30	14.00	0.064	Ar et al. (1974); Harrison (1975); Ar and Rahn (1978)
<i>Taeniopygia guttata</i>	0.32	0.93	15.20	10.60		Serventy and Whittell (1962); Ar and Rahn (1978); Vleck et al. (1979)
<i>Troglodytes aedon</i>	0.53	1.32	16.00	13.00	0.077	Ar et al. (1974); Tullett (1976); Ar and Rahn (1978); Baicich and Harrison (1997)
<i>Turdus merula</i>	1.75	6.36	29.40	21.70	0.117	Harrison (1975); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Turdus migratorius</i>	1.47	6.79	28.00	20.00	0.108	Ar et al. (1974); Carey (1979); Carey et al. (1983); Baicich and Harrison (1997)
<i>Vermivora celata</i>	0.31	1.31	16.52	12.78		Sogge et al. (1994); Conway (1998)

<i>Vermivora virginiae</i>	0.28	1.20	15.66	12.91		Conway (1998); Olson and Martin (1999)
<i>Xanthocephalus xanthocephalus</i>	1.14	4.50	25.77	18.14	0.067	Hanka et al. (1979); Sotherland et al. (1979); Twedt and Crawford (1995)
Pelecaniformes						
<i>Anhinga anhinga</i>	6.12	36.34	53.95	34.95	0.302	Schonwetter (1960-1967); Ar and Rahn (1985); Colacino et al. (1985)
<i>Fregata minor</i>	7.50	89.10	67.75	46.50	0.370	Schonwetter (1960-1967); Whittow (1983); Whittow et al. (2003)
<i>Phalacrocorax auritus</i>	6.42	52.43	60.63	38.08	0.397	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978, 1985)
<i>Phalacrocorax pelagicus</i>	6.77	39.45	57.50	36.65	0.350	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
<i>Sula leucogaster</i>	7.64	67.80	60.35	40.75	0.390	Schonwetter (1960-1967); Ar and Rahn (1978); Whittow (1980, 1983)
<i>Sula sula</i>	6.00	58.29	62.52	40.67	0.380	Schonwetter (1960-1967); Whittow (1983); Whittow et al. (1989)
Phaethontidae						
<i>Phaethon rubricauda</i>	9.56	67.70	66.30	46.33	0.360	Schonwetter (1960-1967); Ar and Rahn (1978); Whittow (1980, 1983)
Phoenicopteriformes						

<i>Phoenicopterus andinus</i>	21.20		89.00	54.30	0.403	Schonwetter (1960-1967); French and Board (1983)
Piciformes						
<i>Dendrocopos syriacus</i>	2.09	5.40	26.10	18.90	0.140	Schonwetter (1960-1967); Ar and Rahn (1985)
Podicipediformes						
<i>Aechmophorus occidentalis</i>	21.64	49.37	58.10	37.70	0.339	Schonwetter (1960-1967); Ar and Rahn (1985)
<i>Podiceps cristatus</i>	19.48	41.10	55.63	35.90	0.264	Schonwetter (1960-1967); Lomholt (1976); Tanaka pers. obs.
<i>Podiceps nigricollis</i>	9.32	21.90	44.13	30.15	0.260	Schonwetter (1960-1967); Sotherland et al. (1984); Boe (1994); Cullen et al. (1999)
<i>Podilymbus podiceps</i>	12.65	21.30	44.20	30.18	0.240	Schonwetter (1960-1967); Ackerman and Platter-Rieger (1979); Davis et al. (1984); Ar and Rahn (1985)
Procellariiformes						
<i>Bulweria bulwerii</i>	2.53	21.08	42.30	30.70	0.138	Schonwetter (1960-1967); Whittow and Pettit (2000)
<i>Fulmarus glacialis</i>	12.40	100.90	72.83	50.05	0.413	Schonwetter (1960-1967); Rahn et al. (1984)
<i>Oceanodroma furcata</i>	2.10	12.60	34.60	26.16	0.135	Schonwetter (1960-1967); Boersma and Wheelwright (1979); Vleck and Kenagy

						(1980)
<i>Oceanodroma leucorhoa</i>	1.55	10.50	32.20	23.60	0.130	Schonwetter (1960-1967); Ar and Rahn (1985); Rahn and Huntington (1988)
<i>Phoebastria immutabilis</i>	32.00	284.80	108.00	69.00	0.491	Schonwetter (1960-1967); Grant et al. (1982b)
<i>Phoebastria nigripes</i>	32.50	304.90	108.15	70.00	0.532	Schonwetter (1960-1967); Grant et al. (1982b)
<i>Pterodroma hypoleuca</i>	5.20	39.50	49.45	37.35	0.181	Schonwetter (1960-1967); Grant et al. (1982a)
<i>Pterodroma phaeopygia</i>	8.82	76.87	63.13	44.84	0.200	Schonwetter (1960-1967); Simons (1983); Whittow et al. (1984)
<i>Puffinus pacificus</i>	6.27	58.17	62.50	41.80	0.250	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1978, 1985); Whittow (1980, 1983)
<i>Puffinus tenuirostris</i>	10.65	80.20	71.60	47.10	0.268	Schonwetter (1960-1967); Tyler (1969); Fitzherbert (1985)
Psittaciformes						
<i>Agapornis personatus</i>	0.58	3.82	22.65	17.00		Mackworth-Praed and Grant (1957); Schonwetter (1960-1967); Bucher (1983)
<i>Agapornis roseicollis</i>	0.97	4.22	23.65	17.45		Schonwetter (1960-1967); McLachlan and Liversidge (1970); Bucher (1983)

<i>Bolborhynchus lineola</i>	1.75	3.88	19.50	19.20		Schonwetter (1960-1967); Bucher (1983)
<i>Enicognathus ferrugineus</i>	2.22	10.26	30.25	24.75		Schonwetter (1960-1967); Bucher (1983)
<i>Melopsittacus undulatus</i>	0.57	2.25	18.10	14.80	0.120	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)
Pteroclididae						
<i>Pterocles namaqua</i>	2.15	9.79	35.60	25.00	0.124	Schonwetter (1960-1967); Thomas and Maclean (1981)
<i>Pterocles orientalis</i>	2.26	27.70	46.75	32.40	0.250	Schonwetter (1960-1967); Ar and Rahn (1985)
Sphenisciformes						
<i>Aptenodytes patagonicus</i>	26.65	302.30	104.35	74.80	0.805	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1985); Handrich (1989)
<i>Pygoscelis adeliae</i>	14.03	122.30	69.80	55.77	0.593	Schonwetter (1960-1967); Rahn and Hammel (1982); Ar and Rahn (1985); Thompson and Goldie (1990)
<i>Spheniscus demersus</i>	15.00	100.75	69.00	52.00	0.524	Schonwetter (1960-1967); Tullett (1976); Ar and Rahn (1985)
Strigiformes						
<i>Bubo bubo</i>	11.30	69.30	58.25	47.36	0.350	Schonwetter (1960-1967); Ar and Rahn (1978, 1985)

<i>Strix aluco</i>	6.15	36.10	48.30	40.40	0.270	Schonwetter (1960-1967); Ar and Rahn (1978, 1985); Tanaka pers. obs.
<i>Tyto alba</i>	5.10	18.70	41.09	31.85	0.230	Schonwetter (1960-1967); Ar and Rahn (1985)
Struthioniformes						
<i>Apteryx australis</i>	26.00	350.20	127.93	79.18	0.431	Schonwetter (1960-1967); Calder III (1978); Calder III et al. (1978); Reid (1981); Silyn-Roberts (1983); McLennan (1988)
<i>Dromaius novaehollandiae</i>	50.59	585.72	132.65	90.03	1.030	Ar et al. (1974); Tullett (1976); Ar and Rahn (1978); Vleck et al. (1980); Beutel et al. (1984); Buttemer et al. (1988); Marchant and Higgins (1990); Dzialowski and Sotherland (2004)
<i>Rhea americana</i>	77.70	609.13	129.07	88.03	0.705	Schonwetter (1960-1967); Thomson (1964); Rossi (1970); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978)
<i>Rhea pennata</i>	74.10	620.00	124.75	87.20	0.800	Schonwetter (1960-1967); Cannon et al. (1986)

<i>Struthio camelus</i>	152.54	1487.49	159.25	129.00	1.884	Schonwetter (1960-1967); Ar et al. (1974); Tullett (1976); Ar and Rahn (1978); Hoyt et al. (1978); Swart et al. (1987); Toien et al. (1988); Meir and Ar (1990); Deeming (1995); Ar et al. (1996); Christensen et al. (1996); Tazawa et al. (1998); Gefen and Ar (2001); Sahan et al. (2003)
Tinamiformes						
<i>Eudromia elegans</i>	7.75	35.80	48.57	40.04	0.230	Schonwetter (1960-1967); Ar and Rahn (1985); Davies (2002)
Crocodylia						
<i>Alligator mississippiensis</i>	51.59	72.27	74.00	43.00	0.352	Packard et al. (1979); Ferguson (1985); Wink et al. (1990)
<i>Crocodylus acutus</i>	21.00	80.00	72.00	44.00	0.600	Lutz et al. (1980); Ferguson (1985)
<i>Crocodylus porosus</i>	31.84	78.31	79.50	51.50	0.386	Ferguson (1985); Grigg and Beard (1985); Tanaka pers. obs.

APPENDIX B: LOG-SCALED VARIABLES FOR DATA FROM APPENDIX A

<i>Species</i>	log G _{H2O}	log M	log A _s	log V _{shell}
Accipitridae				
<i>Aquila rapax</i>	1.114	1.968	4.020	3.736
<i>Buteo rufinus</i>	0.797	1.783	3.886	3.455
<i>Gyps fulvus</i>	1.267	2.386	4.236	4.068
Anseriformes				
<i>Aix galericulata</i>	0.746	1.587	3.712	3.092
<i>Aix sponsa</i>	0.812	1.640	3.761	3.266
<i>Anas acuta</i>	0.556	1.653	3.775	3.211
<i>Anas americana</i>	0.857	1.633	3.777	
<i>Anas bahamensis</i>	0.929	1.543	3.725	3.077
<i>Anas capensis</i>	0.964	1.489	3.803	3.234
<i>Anas carolinensis</i>	0.415	1.401	3.661	3.068
<i>Anas castanea</i>	1.064	1.602	3.738	3.161
<i>Anas chlorotis</i>	1.223	1.792	3.859	
<i>Anas discors</i>	0.663	1.405	3.655	2.996
<i>Anas erythrorhyncha</i>	0.985	1.585	3.733	3.148
<i>Anas falcata</i>	0.857	1.616	3.798	3.229
<i>Anas flavirostris</i>	0.778	1.458	3.755	3.170
<i>Anas fulvigula</i>	1.223	1.747	3.843	3.290
<i>Anas gracilis</i>	0.886	1.530	3.720	3.135
<i>Anas luzonica</i>	1.140	1.708	3.754	
<i>Anas melleri</i>	1.210	1.721	3.817	
<i>Anas penelope</i>	0.763	1.606	3.780	3.195
<i>Anas platalea</i>	0.892	1.543	3.781	3.087
<i>Anas platyrhynchos</i>	1.192	1.923	3.828	3.340
<i>Anas p. diazi</i>	1.059	1.716	3.825	3.256
<i>Anas p. platyrhynchos</i>	1.111	1.833	3.825	3.223

<i>Anas puna</i>	0.855	1.635	3.779	3.211
<i>Anas poecilorhyncha</i> <i>poecilorhyncha</i>	0.968	1.756	3.834	
<i>Anas p. zonorhyncha</i>	1.114		3.823	
<i>Anas rhynchotis rhynchotis</i>	0.690	1.633	3.776	
<i>Anas sibilatrix</i>	0.898	1.724	3.831	
<i>Anas smithii</i>	0.863	1.559	3.773	3.220
<i>Anas sparsa sparsa</i>	1.000	1.857	3.901	
<i>Anas versicolor</i>	0.724	1.501	3.687	3.149
<i>Anas wyvilliana</i>	0.978	1.699	3.796	3.227
<i>Anser albifrons flavirostris</i>	1.188	2.068	4.045	
<i>Anser a. frontalis</i>	1.367	2.124	4.060	3.569
<i>Anser a. gambelli</i>	1.348	2.124	4.070	
<i>Anser anser</i>	1.474	2.221	4.117	3.893
<i>Anser brachyrhynchus</i>	1.396	2.120	4.049	3.749
<i>Anser cygnoides</i>	1.489	2.168	4.100	3.772
<i>Anser erythropus</i>	1.346	2.105	4.000	3.653
<i>Anser fabalis</i>	1.364	2.203	4.101	3.753
<i>Anser f. rossicus</i>	1.528	2.164		
<i>Anser indicus</i>	1.230	2.097	4.088	3.769
<i>Aythya affinis</i>	0.903	1.708	3.808	3.308
<i>Aythya americana</i>	1.143	1.815	3.870	3.482
<i>Aythya baeri</i>	0.672	1.633	3.759	
<i>Aythya fuligula</i>	0.959	1.748	3.835	
<i>Aythya marila mariloides</i>	1.137	1.826	3.878	
<i>Aythya novaeseelandiae</i>	1.044	1.801	3.903	3.350
<i>Aythya nyroca</i>	0.924	1.633	3.762	
<i>Aythya valisineria</i>	1.201	1.833	3.885	
<i>Biziura lobata</i>	1.338	2.107	4.061	
<i>Branta canadensis</i>	1.486	2.195	4.123	3.839

<i>Branta c. parvipes</i>	1.560	1.959	4.061	
<i>Branta hutchinsii leucopareia</i>	1.352	2.021	4.055	3.657
<i>Branta h. minima</i>	1.239	2.003	3.987	3.543
<i>Branta leucopsis</i>	1.336	2.037	4.027	3.615
<i>Branta ruficollis</i>	1.023	1.917	3.976	3.600
<i>Branta sandvicensis</i>	1.531	2.170	4.069	3.671
<i>Bucephala albeola</i>	0.708	1.551	3.721	3.277
<i>Bucephala clangula</i>	1.025	1.782	3.861	3.292
<i>Bucephala islandica</i>	1.027	1.837	3.898	3.489
<i>Cairina moschata</i>	1.087	1.894	3.918	3.520
<i>Cairina scutulata</i>	1.329	1.932	3.905	3.496
<i>Callonetta leucophrys</i>	0.767	1.502	3.680	
<i>Cereopsis novaehollandiae</i>	1.237	2.099	4.066	3.753
<i>Chen caerulescens atlantica</i>	1.400	2.104	4.061	3.802
<i>Chen canagica</i>	1.402	2.107	4.044	3.743
<i>Chen rossii</i>	1.270	1.963	3.977	3.482
<i>Chenonetta jubata</i>	0.851	1.732	3.823	
<i>Chloephaga melanoptera</i>	1.075	2.049	4.007	3.650
<i>Chloephaga picta leucoptera</i>	1.377	2.026	4.001	3.624
<i>Chloephaga p. picta</i>	1.292	2.086	4.050	
<i>Chloephaga poliocephala</i>	1.009	1.975	3.966	3.522
<i>Chloephaga rubidiceps</i>	1.068	1.925	3.969	3.474
<i>Clangula hyemalis</i>	1.064	1.662	3.779	3.203
<i>Cyanochen cyanoptera</i>	1.177	1.922	3.988	3.450
<i>Cygnus columbianus bewickii</i>	1.589	2.415	4.241	4.122
<i>Cygnus melanocoryphus</i>	1.622	2.393	4.233	
<i>Cygnus olor</i>	1.818	2.542	4.310	4.123
<i>Dendrocygna arborea</i>	1.152	1.775	3.820	3.433
<i>Dendrocygna arcuata</i>	0.785	1.562	3.743	3.323
<i>Dendrocygna autumnalis</i>	1.063	1.636	3.751	3.282

<i>Dendrocygna bicolor</i>	1.216	1.728	3.806	3.338
<i>Dendrocygna guttata</i>	1.072	1.699	3.801	
<i>Dendrocygna viduata</i>	0.919	1.556	3.708	
<i>Heteronetta atricapilla</i>	1.272	1.778	3.870	
<i>Lophodytes cucullatus</i>	0.923	1.739	3.843	3.515
<i>Marmaronetta angustirostris</i>	0.973	1.491	3.668	
<i>Merganetta armata armata</i>	1.017	1.758	3.857	
<i>Mergellus albellus</i>	0.959	1.623	3.754	
<i>Mergus merganser merganser</i>	1.175	1.840	3.940	3.445
<i>Mergus serrator</i>	0.773	1.836	3.912	3.417
<i>Neochen jubata</i>	1.029	1.799	3.863	
<i>Netta peposaca</i>	1.199	1.730	3.825	3.427
<i>Netta rufina</i>	0.964	1.739	3.834	3.366
<i>Oxyura jamaicensis</i>	1.306	1.866	3.907	3.550
<i>Oxyura leucocephala</i>	1.344	1.979	3.981	3.549
<i>Oxyura maccoa</i>	1.384	1.982	3.981	
<i>Oxyura vittata</i>	1.356	1.940	3.953	3.634
<i>Sarkidiornis melanotos melanotos</i>	0.919	1.820	3.878	3.325
<i>Somateria fischeri</i>	1.265	1.863	3.913	3.376
<i>Somateria mollissima</i>	1.268	2.016	4.028	3.608
<i>Somateria m. mollissima</i>	1.314	2.042	4.030	3.574
<i>Somateria spectabilis</i>	1.332	1.863	3.915	
<i>Tadorna ferruginea</i>	1.151	1.909	3.947	3.549
<i>Tadorna tadorna</i>	1.180	1.899	3.940	3.542
<i>Tadorna variegata</i>	1.108	1.958	3.960	3.573
<i>Thalassornis leuconotus leuconotus</i>	1.338	1.924	3.948	
Caprimulgiformes				
<i>Chordeiles acutipennis</i>	-0.036	0.760	3.206	2.359

Cathartidae				
<i>Vultur gryphus</i>	1.356	2.507	4.261	4.047
Charadriiformes				
<i>Anous minutus marcusii</i>	0.661	1.370	3.605	2.883
<i>Anous stolidus pileatus</i>	0.796	1.579	3.740	3.111
<i>Burhinus oedicephalus</i>	0.660	1.525	3.741	3.172
<i>Charadrius alexandrinus</i>	0.090	0.874	3.320	2.516
<i>Charadrius vociferus</i>	0.320	1.155	3.483	2.683
<i>Chlidonias leucopterus</i>	0.350	1.146	3.410	2.556
<i>Chlidonias niger</i>	0.573	1.026	3.403	2.517
<i>Fratercula arctica</i>	0.903	1.776	3.881	3.372
<i>Fratercula cirrhata</i>	1.114	1.954	3.981	3.527
<i>Gelochelidon nilotica</i>	0.792	1.452	3.679	3.003
<i>Glareola pratincola</i>	0.337	0.926	3.353	2.530
<i>Gygis alba</i>	0.540	1.330	3.585	2.821
<i>Haematopus ostralegus</i>	0.833	1.618	3.809	3.212
<i>Himantopus mexicanus</i>	0.731	1.322	3.590	2.940
<i>Larus argentatus</i>	1.226	1.947	3.987	3.454
<i>Larus atricilla</i>	0.957	1.651	3.775	3.173
<i>Larus canus</i>	1.123	1.755	3.850	3.235
<i>Larus fuscus</i>	1.203	1.927	3.946	3.423
<i>Larus glaucescens</i>	1.365	1.989	4.000	3.544
<i>Larus heermanni</i>	1.027	1.729	3.847	3.280
<i>Larus livens</i>	1.293	1.990	3.999	3.519
<i>Larus marinus</i>	1.300	2.050	4.011	3.579
<i>Larus modestus</i>	0.568	1.690	3.833	3.215
<i>Larus ridibundus</i>	0.940	1.551	3.746	3.085
<i>Larus serranus</i>	0.914	1.744	3.850	3.294
<i>Limosa limosa</i>	0.978	1.592	3.750	3.044
<i>Numenius arquata</i>	1.210	1.918	3.955	3.332

<i>Numenius phaeopus</i>	0.989	1.728	3.843	3.144
<i>Onychoprion fuscatus</i>	0.831	1.538	3.721	3.083
<i>Onychoprion lunatus</i>	0.657	1.458	3.628	2.832
<i>Philomachus pugnax</i>	0.559	1.281	3.589	
<i>Pluvialis apricaria</i>	0.700	1.513	3.719	2.949
<i>Pluvianus aegyptius</i>	0.318	0.977	3.343	2.642
<i>Ptychoramphus aleuticus</i>	0.611	1.473	3.665	3.007
<i>Recurvirostra americana</i>	0.685	1.511	3.684	3.057
<i>Rissa tridactyla</i>	0.987	1.705	3.829	3.244
<i>Rynchops niger</i>	0.833	1.422	3.640	2.957
<i>Stercorarius maccormicki</i>	1.212	2.003	3.989	3.591
<i>Stercorarius skua</i>	1.265	1.980	3.983	3.501
<i>Sterna forsteri</i>	0.509	1.326	3.585	2.899
<i>Sterna hirundo</i>	0.602	1.313	3.578	2.857
<i>Sterna paradisaea</i>	0.705	1.262	3.554	2.758
<i>Sternula albifrons</i>	0.280	0.944	3.338	2.452
<i>Thalasseus elegans</i>	0.996	1.612	3.755	3.218
<i>Thalasseus maximus</i>	1.144	1.835	3.899	3.341
<i>Thalasseus sandvicensis</i>	0.894	1.561	3.722	3.120
<i>Tringa totanus</i>	0.638	1.349	3.615	2.825
<i>Uria aalge</i>	1.302	2.064	3.994	3.774
<i>Uria lomvia</i>	1.238	2.046	4.029	3.773
<i>Vanellus vanellus</i>	0.673	1.423	3.655	2.917
Ciconiiformes				
<i>Ardea albus</i>	0.876	1.689	3.809	3.229
<i>Bubulcus ibis</i>	0.715	1.417	3.648	2.960
<i>Egretta caerulea</i>	0.740	1.427	3.623	2.995
<i>Egretta garzetta</i>	0.858	1.455	3.655	2.995
<i>Egretta thula</i>	0.585	1.354	3.630	2.931
<i>Egretta tricolor</i>	0.591	1.416	3.586	2.938

<i>Eudocimus albus</i>	0.823	1.701	3.804	3.309
<i>Nycticorax nycticorax</i>	0.799	1.528	3.742	3.103
<i>Plegadis falcinellus</i>	0.892	1.572	3.734	3.167
<i>Plegadis ridgwayi</i>	0.716	1.530	3.711	3.217
Columbiformes				
<i>Columba livia</i>	0.576	1.231	3.488	2.767
<i>Streptopelia decaocto</i>	0.405	0.872	3.340	2.454
<i>Streptopelia roseogrisea</i>	0.346	0.905	3.280	2.360
<i>Streptopelia senegalensis</i>	0.328	0.822	3.202	2.282
<i>Streptopelia turtur</i>	0.344	0.919	3.286	2.432
<i>Zenaida macroura</i>	0.271	0.888	3.245	2.388
Coraciiformes				
<i>Merops ornatus</i>	0.076	0.633	3.103	2.037
Falconidae				
<i>Falco naumanni</i>	0.447	1.034	3.472	2.755
<i>Falco tinnunculus</i>	0.600	1.258	3.566	2.903
Galliformes				
<i>Alectoris graeca</i>	0.529	1.260	3.572	3.019
<i>Alectura lathami</i>	1.681	2.288	4.155	3.665
<i>Ammoperdix heyi</i>	0.072	1.154	3.461	2.751
<i>Bonasa umbellus togata</i>	0.640	1.274	3.548	
<i>Chrysolophus amherstiae</i>	0.774	1.478	3.676	3.091
<i>Chrysolophus pictus</i>	0.783	1.513	3.636	3.050
<i>Coturnix coturnix</i>	0.476	1.022	3.307	2.519
<i>Falcipennis canadensis canace</i>	0.731	1.318	3.594	
<i>Gallus gallus</i>	1.102	1.748	3.871	3.388
<i>Gallus g. bankiva</i>	0.987	1.581	3.701	3.189
<i>Lagopus lagopus</i>	0.465	1.350	3.595	2.881
<i>Lagopus leucura</i>	0.398		3.564	2.829
<i>Leipoa ocellata</i>	1.638	2.238	4.142	3.540

<i>Lophophorus impejanus</i>	0.922	1.810	3.902	3.439
<i>Lophura nycthemera</i>	0.966	1.601	3.789	3.363
<i>Lophura swinhoii</i>	0.863	1.617	3.765	3.258
<i>Meleagris gallopavo</i>	1.155	1.921	3.921	3.518
<i>Numida meleagris galeatus</i>	1.000	1.689	3.779	3.471
<i>Pavo cristatus</i>	1.147	1.978	4.009	3.708
<i>Pavo muticus</i>	1.304	2.001	4.039	3.775
<i>Phasianus colchicus</i>	0.835	1.506	3.659	3.119
<i>Syrnaticus soemmerringii</i>	0.899	1.498	3.681	3.087
Gaviiformes				
<i>Gavia immer</i>	1.991	2.188	4.129	3.893
Gruiformes				
<i>Fulica americana</i>	0.843	1.558	3.728	3.208
<i>Fulica atra</i>	1.157	1.603	3.708	3.131
<i>Gallinula tenebrosa</i>	0.996	1.524	3.706	3.137
<i>Porphyrio porphyrio</i>	0.979	1.546	3.735	3.106
Passeriformes				
<i>Agelaius phoeniceus</i>	0.129	0.628	3.134	2.111
<i>Carduelis tristis</i>	-0.252	0.182	2.771	1.584
<i>Cercotrichas galactotes</i>	-0.135	0.362	3.039	1.942
<i>Cinnyris osea</i>	-0.509	-0.066	2.719	1.418
<i>Dendroica petechia</i>	-0.347	0.204	2.832	2.008
<i>Ficedula hypoleuca</i>	-0.197	0.204	2.866	1.539
<i>Galerida cristata</i>	-0.036	0.467	3.064	2.064
<i>Hippolais rama</i>	-0.509		2.775	
<i>Hirundo rustica</i>	-0.480	0.255	2.885	1.648
<i>Junco hyemalis</i>	-0.208	0.369	2.970	1.839
<i>Menura novaehollandiae</i>	0.850	1.789	3.777	3.115
<i>Molothrus ater</i>	0.029	0.522	3.011	2.122
<i>Muscicapa striata</i>	-0.208	0.270	2.903	1.806

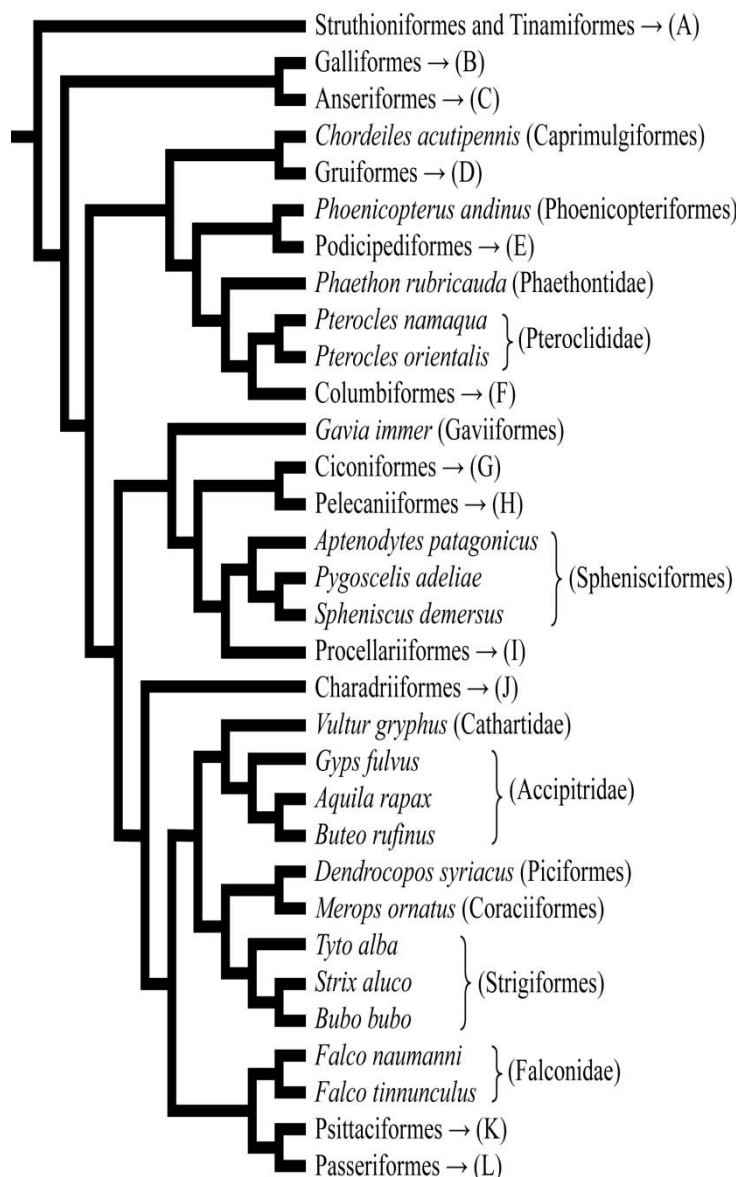
<i>Passer ammodendri</i>	-0.180		2.927	
<i>Passer domesticus</i>	-0.079	0.432	3.029	2.038
<i>Passer moabiticus</i>	-0.268	0.176	2.881	1.836
<i>Pica pica</i>	0.091	0.973	3.369	2.441
<i>Ploceus capensis</i>	-0.079	0.560	3.090	
<i>Ploceus cucullatus</i>	-0.076	0.450	3.036	
<i>Prinia gracilis</i>	-0.432	0.049	2.659	1.504
<i>Pycnonotus capensis</i>	-0.004	0.484	3.085	1.988
<i>Quiscalus quiscula</i>	0.474	0.799	3.249	2.342
<i>Riparia riparia</i>	-0.384	0.176	2.834	1.557
<i>Scotocerca inquieta</i>	-0.229		2.722	
<i>Serinus canaria</i>	-0.208	0.204	2.847	
<i>Sylvia curruca</i>	-0.509	0.155	2.803	
<i>Sylvia mystacea</i>	-0.678		2.838	
<i>Tachycineta bicolor</i>	-0.301	0.236	2.916	1.723
<i>Taeniopygia guttata</i>	-0.495	-0.034	2.694	
<i>Troglodytes aedon</i>	-0.280	0.121	2.808	1.691
<i>Turdus merula</i>	0.243	0.803	3.283	2.351
<i>Turdus migratorius</i>	0.167	0.832	3.226	2.259
<i>Vermivora celata</i>	-0.509	0.117	2.813	
<i>Vermivora virginiae</i>	-0.553	0.079	2.796	
<i>Xanthocephalus xanthocephalus</i>	0.058	0.653	3.149	1.975
Pelecaniformes				
<i>Anhinga anhinga</i>	0.787	1.560	3.726	3.206
<i>Fregata minor</i>	0.875	1.950	3.941	3.509
<i>Phalacrocorax auritus</i>	0.808	1.720	3.806	3.404
<i>Phalacrocorax pelagicus</i>	0.831	1.596	3.770	3.314
<i>Sula leucogaster</i>	0.883	1.831	3.838	3.429
<i>Sula sula</i>	0.778	1.766	3.848	3.428
Phaethontidae				

<i>Phaethon rubricauda</i>	0.980	1.831	3.932	3.489
<i>Phoenicopterus andinus</i>	1.326		4.094	3.699
Piciformes				
<i>Dendrocopos syriacus</i>	0.320	0.732	3.173	2.319
Podicipediformes				
<i>Aechmophorus occidentalis</i>	1.335	1.693	3.787	3.318
<i>Podiceps cristatus</i>	1.290	1.614	3.749	3.171
<i>Podiceps nigricollis</i>	0.969	1.340	3.587	3.002
<i>Podilymbus podiceps</i>	1.102	1.328	3.588	2.968
Procellariiformes				
<i>Bulweria bulwerii</i>	0.403	1.324	3.581	2.721
<i>Fulmarus glacialis</i>	1.093	2.004	3.999	3.615
<i>Oceanodroma furcata</i>	0.321	1.100	3.432	2.562
<i>Oceanodroma leucorhoa</i>	0.190	1.021	3.356	2.470
<i>Phoebastria immutabilis</i>	1.505	2.455	4.267	3.958
<i>Phoebastria nigripes</i>	1.512	2.484	4.275	4.001
<i>Pterodroma hypoleuca</i>	0.716	1.597	3.731	2.988
<i>Pterodroma phaeopygia</i>	0.945	1.886	3.901	3.202
<i>Puffinus pacificus</i>	0.797	1.765	3.862	3.260
<i>Puffinus tenuirostris</i>	1.027	1.904	3.963	3.391
Psittaciformes				
<i>Agapornis personatus</i>	-0.237	0.582	3.069	
<i>Agapornis roseicollis</i>	-0.013	0.625	3.098	
<i>Bolborhynchus lineola</i>	0.243	0.589	3.066	
<i>Enicognathus ferrugineus</i>	0.346	1.011	3.355	
<i>Melopsittacus undulatus</i>	-0.244	0.352	2.916	1.996
Pteroclididae				
<i>Pterocles namaqua</i>	0.332	0.991	3.420	2.514
<i>Pterocles orientalis</i>	0.354	1.442	3.641	3.039
Sphenisciformes				

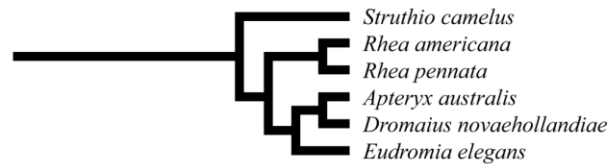
<i>Aptenodytes patagonicus</i>	1.426	2.480	4.307	4.213
<i>Pygoscelis adeliae</i>	1.147	2.087	4.045	3.818
<i>Spheniscus demersus</i>	1.176	2.003	4.004	3.724
Strigiformes				
<i>Bubo bubo</i>	1.053	1.841	3.904	3.448
<i>Strix aluco</i>	0.789	1.558	3.762	3.193
<i>Tyto alba</i>	0.708	1.272	3.588	2.950
Struthioniformes				
<i>Apteryx australis</i>	1.415	2.544	4.372	4.006
<i>Dromaius novaehollandiae</i>	1.704	2.768	4.455	4.468
<i>Rhea americana</i>	1.890	2.785	4.438	4.286
<i>Rhea pennata</i>	1.870	2.792	4.428	4.331
<i>Struthio camelus</i>	2.183	3.172	4.706	4.981
Tinamiformes				
<i>Eudromia elegans</i>	0.889	1.554	3.759	3.121
Crocodylia				
<i>Alligator mississippiensis</i>	1.713	1.859	3.942	3.488
<i>Crocodylus acutus</i>	1.322	1.903	3.944	3.722
<i>Crocodylus porosus</i>	1.503	1.894	4.060	3.646

APPENDIX C: CLADOGRAM OF 285 LIVING BIRD TAXA, USED FOR PHYLOGENETICALLY-CORRECTED ANCOVAS (CHAPTER FOUR)

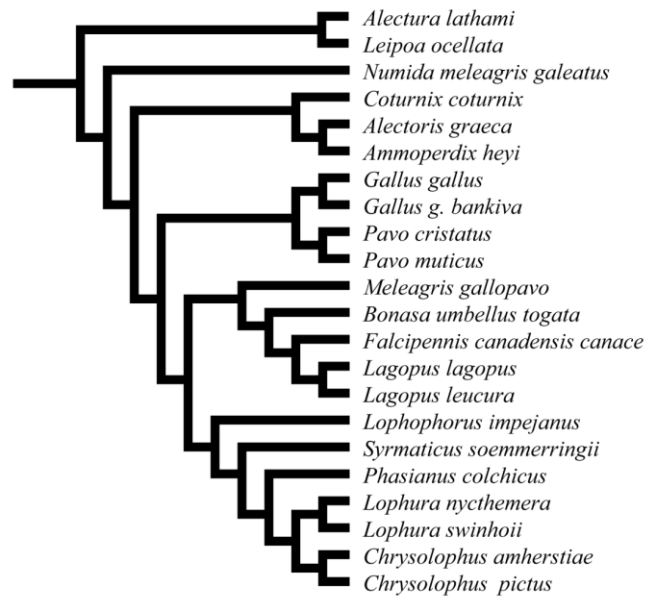
The phylogenetic tree is a composite from Sheldon (1987), Livezey (1995, 1996), Sheldon and Slikas (1997), Kennedy and Spencer (2000), Sheldon et al. (2000), Wink and Heidrich (2000), Johnson et al. (2001), Kennedy and Page (2002), de Kloet and de Kloet (2005), Fjeldsa (2004), Thomas et al. (2004), Bertelli and Giannini (2005), Lerner and Mindell (2005), Crowe et al. (2006), Ericson et al. (2006), Jonsson and Fjeldsa (2006), Ksepka et al. (2006), Griffiths et al. (2007), Hackett et al. (2008), Wright et al. (2008), Gonzalez et al. (2009), Mayr (2010), McCracken et al. (2010), Smith (2010), Yang et al. (2010).



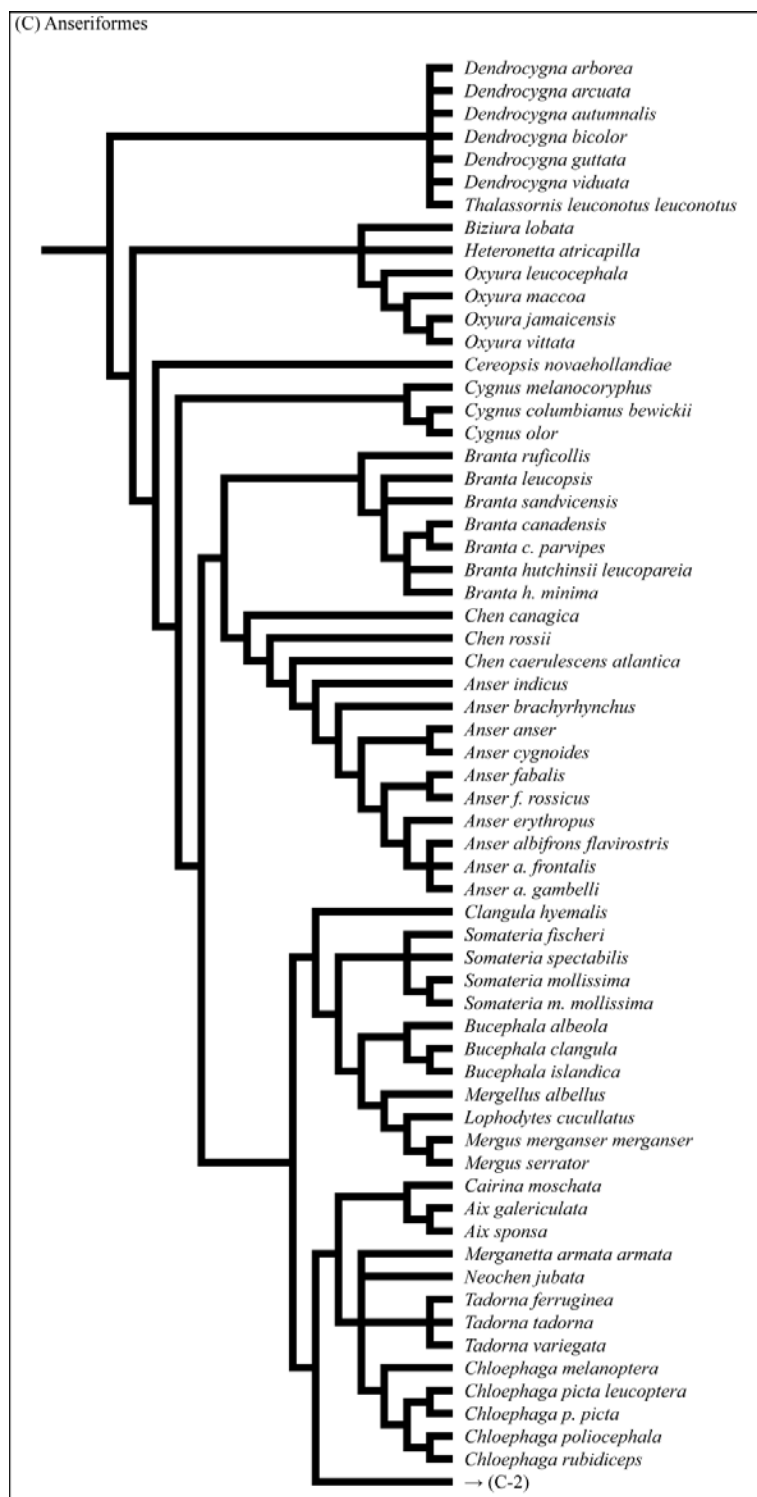
Appendix C. Continued.

(A) Struthioniformes and Tinamiformes (*Eudromia*)

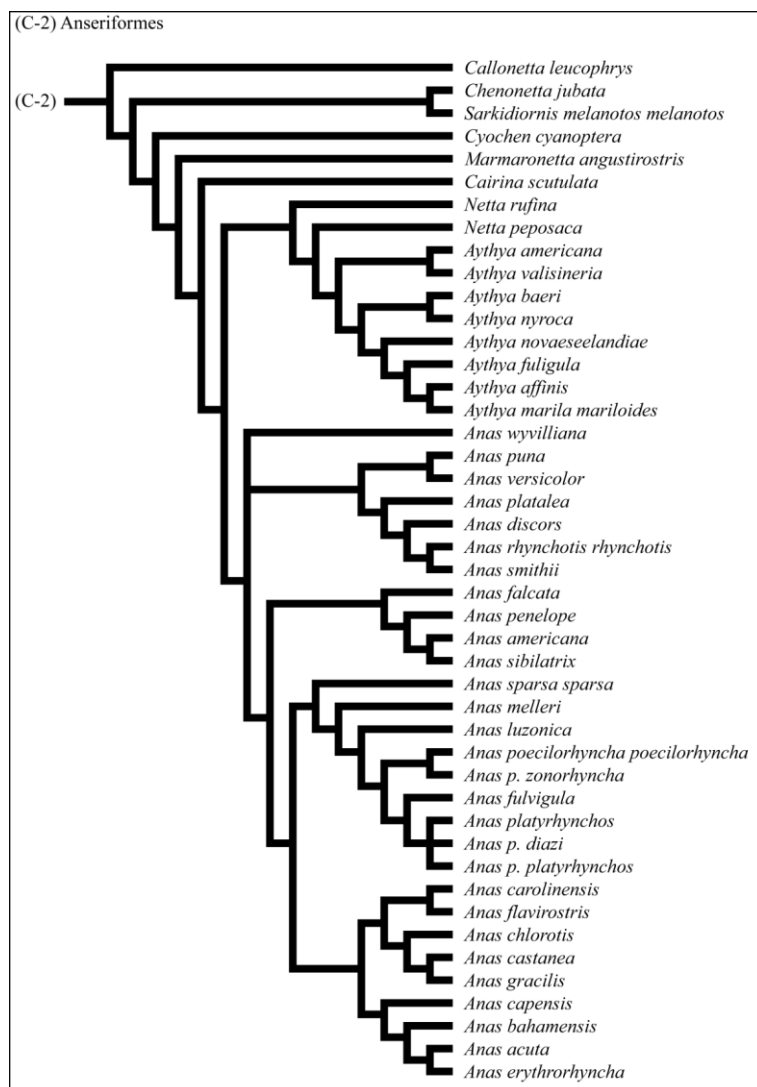
(B) Galliformes



Appendix C. Continued.

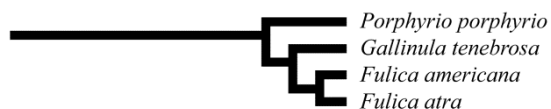


Appendix C. Continued.



Appendix C. Continued.

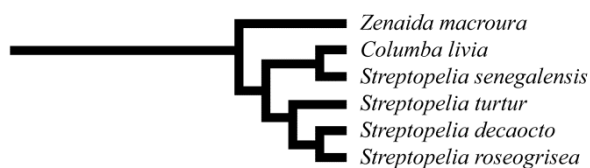
(D) Gruiformes



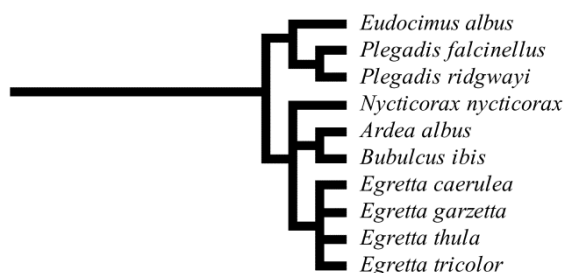
(E) Podicipediformes



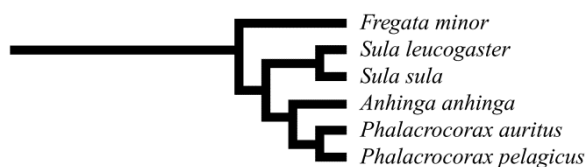
(F) Columbiformes



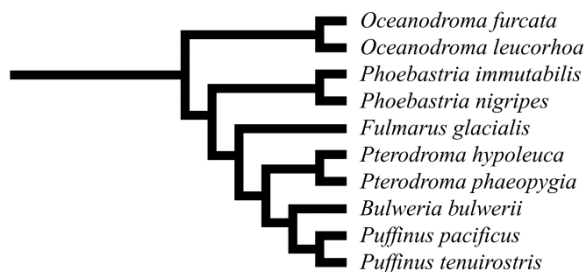
(G) Ciconiiformes



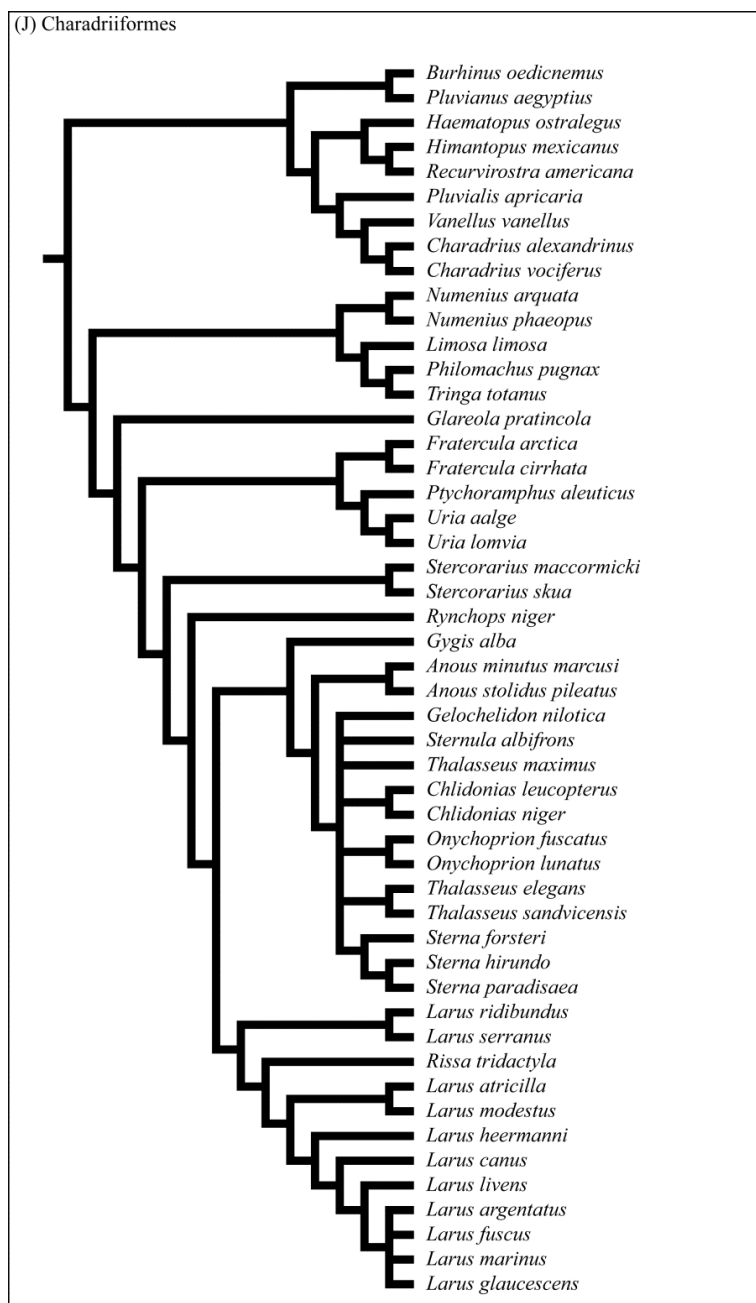
(H) Pelecaniiformes



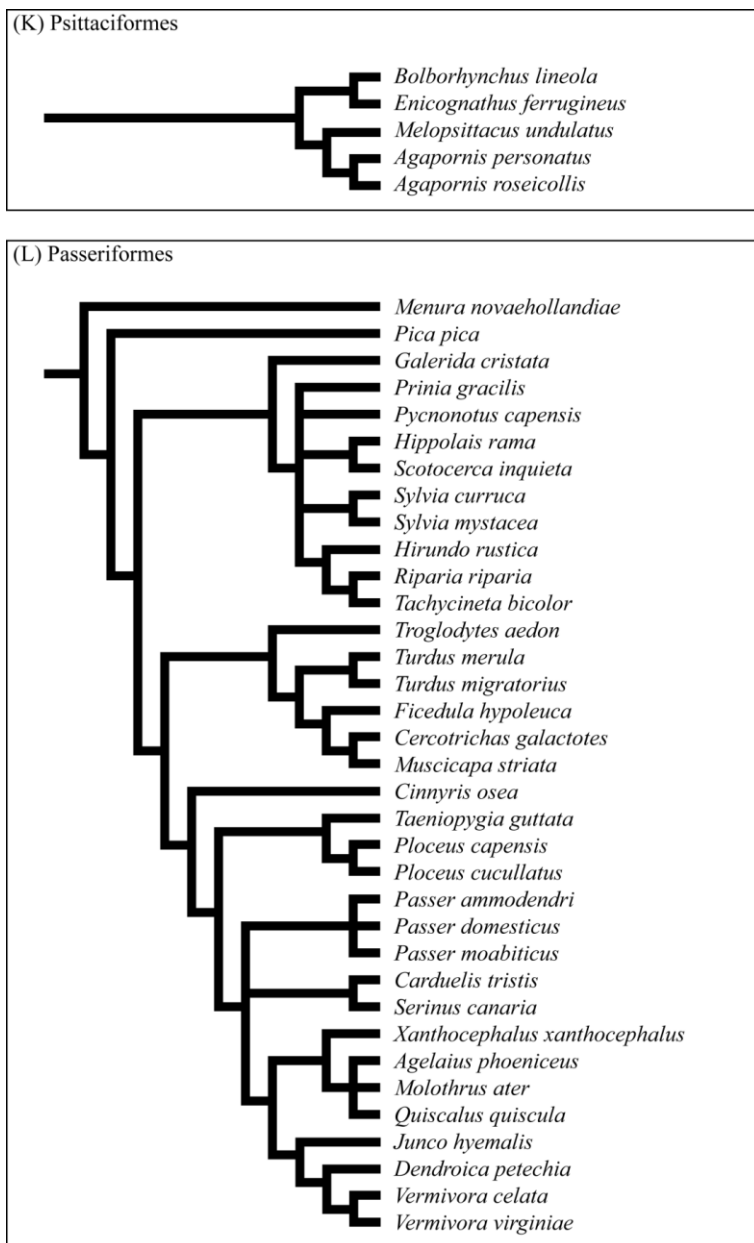
(I) Procellariiformes



Appendix C. Continued.



Appendix C. Continued.



APPENDIX D: NESTER TYPES OF 285 LIVING BIRD TAXA

Nester type is based on nest structure and location from Hansell (2000). Nester type: H, humid nester; R, regular nester. Nest location: 1, tree/bush; 2, grass/reeds; 3, on the ground; 4, tree hole/cavity; 5, ground hole/cavity; 6, on wall; 7, on ledge; 8, on water; 9, King Penguin type. Nest structure: 1, cup; 2, dome; 3, dome and tube; 4, plate; 5, bed; 6, scrape; 7, mound; 8, burrow; 9, King Penguin type. King Penguin type is new for this study, and it has an exceptional incubation style as it incubates eggs between parent feet. *Indicates nest structure was referred from other similar species of same genus.

<i>Species</i>	Type	Nest Location	Nest structure	Sources
Accipitridae				
<i>Aquila rapax</i>	R	1	4	Harrison (1975)
<i>Buteo rufinus</i>	R	1/7	4/5	del Hoyo et al. (1994); Hayman and Hume (2007)
<i>Gyps fulvus</i>	R	5	5	Harrison (1975)
Anseriformes				
<i>Aix galericulata</i>	R	4	5	Harrison (1975); Kear (2005)
<i>Aix sponsa</i>	R	4	5	Delacour (1959); Hepp and Bellrose (1995); Baicich and Harrison (1997)
<i>Anas acuta</i>	R	3	5	Baicich and Harrison (1997)
<i>Anas americana</i>	R	3	5	Baicich and Harrison (1997)
<i>Anas bahamensis</i>	R	3	5	Kear (2005)

<i>Anas capensis</i>	R	3	5	McLachlan and Liversidge (1970)
<i>Anas carolinensis</i>	R	3	5	del Hoyo et al. (1992)
<i>Anas castanea</i>	R	4/5	5	Pizzey (1980)
<i>Anas chlorotis</i>	R	3	5	del Hoyo et al. (1992)
<i>Anas discors</i>	R	3	5	Baicich and Harrison (1997)
<i>Anas erythrorhyncha</i>	R	3	5	del Hoyo et al. (1992); Kear (2005)
<i>Anas falcata</i>	R	3	5	Phillips (1923); Kear (2005)
<i>Anas flavirostris</i>	R	3/5	5	Delacour (1956); Kear (2005)
<i>Anas fulvigula</i>	R	3	5	Bellrose (1976)
<i>Anas gracilis</i>	R	3/4	5	Serventy and Whittell (1962); Pizzey (1980)
<i>Anas luzonica</i>	R	3	5	Temme (1976); del Hoyo et al. (1992)
<i>Anas melleri</i>	R	3	5	del Hoyo et al. (1992)
<i>Anas penelope</i>	R	3	5	del Hoyo et al. (1992)
<i>Anas platalea</i>	R	3	5	Kear (2005)
<i>Anas platyrhynchos</i>	R	3/4	4/5	Kear (2005)
<i>Anas p. diazi</i>	R	3	5	Bellrose (1976)
<i>Anas p. platyrhynchos</i>	R	3	5	Harrison (1975)
<i>Anas puna</i>	R	3	5	Carey et al. (1989b); del Hoyo et al. (1992)
<i>Anas poecilorhyncha poecilorhyncha</i>	R	3	5	del Hoyo et al. (1992)
<i>Anas p. zonorhyncha</i>	R	3	5	del Hoyo et al. (1992)

<i>Anas rhynchotis rhynchotis</i>	R	3/4	5	Pizzey (1980)
<i>Anas sibilatrix</i>	R	3	5*	del Hoyo et al. (1992)
<i>Anas smithii</i>	R	3	5	McLachlan and Liversidge (1970); del Hoyo et al. (1992)
<i>Anas sparsa sparsa</i>	R	3	5	del Hoyo et al. (1992)
<i>Anas versicolor</i>	R	3	5	del Hoyo et al. (1992); Kear (2005)
<i>Anas wyvilliana</i>	R	3	5	Kear (2005)
<i>Anser albifrons flavirostris</i>	R	3	5	Baicich and Harrison (1997)
<i>Anser a. frontalis</i>	R	3	5	Baicich and Harrison (1997)
<i>Anser a. gambelli</i>	R	3	5	Baicich and Harrison (1997)
<i>Anser anser</i>	R	3	5/6	Harrison (1975)
<i>Anser brachyrhynchus</i>	R	3	5	Kear (2005)
<i>Anser cygnoides</i>	R	3	5	Kear (2005)
<i>Anser erythropus</i>	R	3	5	Harrison (1975)
<i>Anser fabalis</i>	R	3	5	Harrison (1975)
<i>Anser f. rossicus</i>	R	3	5	Harrison (1975)
<i>Anser indicus</i>	R	1/3/7	4/5	Harrison (1975); del Hoyo et al. (1992)
<i>Aythya affinis</i>	R	3	5	Baicich and Harrison (1997)
<i>Aythya americana</i>	R	3/8	5	Bellrose (1976)
<i>Aythya baeri</i>	R	3	5	Kear (2005)

<i>Aythya fuligula</i>	R	3	5	del Hoyo et al. (1992)
<i>Aythya marila mariloides</i>	R	3	5	Baicich and Harrison (1997)
<i>Aythya novaeseelandiae</i>	R	3	5	Oliver (1955); Kear (2005)
<i>Aythya nyroca</i>	R	3	5	del Hoyo et al. (1992)
<i>Aythya valisineria</i>	R	3/8	5	Baicich and Harrison (1997)
<i>Biziura lobata</i>	R	3/4	5	Pizzey (1980)
<i>Branta canadensis</i>	R	3	5	Harrison (1975)
<i>Branta c. parvipes</i>	R	3	5	Harrison (1975)
<i>Branta hutchinsii leucopareia</i>	R	3	5	Harrison (1975)
<i>Branta h. minima</i>	R	3	5	Harrison (1975)
<i>Branta leucopsis</i>	R	3/7	5	Harrison (1975)
<i>Branta ruficollis</i>	R	3	5	del Hoyo et al. (1992); Hayman and Hume (2007)
<i>Branta sandvicensis</i>	R	3	5	Merne (1974); Banko et al. (1999)
<i>Bucephala albeola</i>	R	3/4	5	Baicich and Harrison (1997)
<i>Bucephala clangula</i>	R	3/4	5	Harrison (1975)
<i>Bucephala islandica</i>	R	5	5	Harrison (1975)
<i>Cairina moschata</i>	R	3/4	5	Baicich and Harrison (1997)
<i>Cairina scutulata</i>	R	4	5	Kear (2005)
<i>Callonetta leucophrys</i>	R	4	5	Kear (2005)
<i>Cereopsis novaehollandiae</i>	R	3	5	Pizzey (1980)

<i>Chen caerulescens atlantica</i>	R	3	5	Baicich and Harrison (1997)
<i>Chen canagica</i>	R	3	5	Bellrose (1976)
<i>Chen rossii</i>	R	3	5	Bellrose (1976)
<i>Chenonetta jubata</i>	R	4	5	Pizzey (1980)
<i>Chloephaga melanoptera</i>	R	3/5	6	Carey et al. (1990); Kear (2005)
<i>Chloephaga picta leucoptera</i>	R	3	5	del Hoyo et al. (1992); Kear (2005)
<i>Chloephaga p. picta</i>	R	3	5	del Hoyo et al. (1992); Kear (2005)
<i>Chloephaga poliocephala</i>	R	3/4	5	del Hoyo et al. (1992); Kear (2005)
<i>Chloephaga rubidiceps</i>	R	3	5	del Hoyo et al. (1992); Kear (2005)
<i>Clangula hyemalis</i>	R	3	5	Harrison (1975)
<i>Cyanochen cyanoptera</i>	R	3	5	del Hoyo et al. (1992); Kear (2005)
<i>Cygnus columbianus bewickii</i>	R	3/8	5	Baicich and Harrison (1997)
<i>Cygnus melanocoryphus</i>	R	3/8	5	del Hoyo et al. (1992)
<i>Cygnus olor</i>	R	3/8	5	del Hoyo et al. (1992)
<i>Dendrocygna arborea</i>	R	1/3/4	4/5	Kear (2005)
<i>Dendrocygna arcuata</i>	R	3	5	Pizzey (1980)
<i>Dendrocygna autumnalis</i>	R	3/4	4/5	Baicich and Harrison (1997)
<i>Dendrocygna bicolor</i>	R	3/4	4/5	Baicich and Harrison (1997)
<i>Dendrocygna guttata</i>	R	3/4/8	5*	del Hoyo et al. (1992)
<i>Dendrocygna viduata</i>	R	3	5	del Hoyo et al. (1992)

<i>Heteronetta atricapilla</i>	R	3/8	5	del Hoyo et al. (1992)
<i>Lophodytes cucullatus</i>	R	4/5	5	Bellrose (1976); del Hoyo et al. (1992)
<i>Marmaronetta angustirostris</i>	R	3	5	del Hoyo et al. (1992)
<i>Merganetta armata armata</i>	R	5	5	del Hoyo et al. (1992)
<i>Mergellus albellus</i>	R	4	5	del Hoyo et al. (1992)
<i>Mergus merganser merganser</i>	R	4/5	5	Harrison (1975)
<i>Mergus serrator</i>	R	4/5	4/5	Harrison (1975)
<i>Neochen jubata</i>	R	4	5	del Hoyo et al. (1992)
<i>Netta peposaca</i>	R	3/8	5	del Hoyo et al. (1992); Kear (2005)
<i>Netta rufina</i>	R	3	5	Harrison (1975)
<i>Oxyura jamaicensis</i>	R	3/8	5	Harrison (1975); del Hoyo et al. (1992)
<i>Oxyura leucocephala</i>	R	3/8	5	Harrison (1975); del Hoyo et al. (1992)
<i>Oxyura maccoa</i>	R	8	5	del Hoyo et al. (1992)
<i>Oxyura vittata</i>	R	3/8	5	del Hoyo et al. (1992); Kear (2005)
<i>Sarkidiornis melanotos melanotos</i>	R	3/4	5	del Hoyo et al. (1992)
<i>Somateria fischeri</i>	R	3	5	Baicich and Harrison (1997)
<i>Somateria mollissima</i>	R	3	5	Harrison (1975)
<i>Somateria m. mollissima</i>	R	3	5	Harrison (1975)
<i>Somateria spectabilis</i>	R	3	5	Baicich and Harrison (1997)
<i>Tadorna ferruginea</i>	R	4/5	5	Harrison (1975)

<i>Tadorna tadorna</i>	R	4/5	5	Harrison (1975)
<i>Tadorna variegata</i>	R	3/4/5/7	5	Williams (1979); del Hoyo et al. (1992)
<i>Thalassornis leuconotus leuconotus</i>	R	3	5	del Hoyo et al. (1992)
Caprimulgiformes				
<i>Chordeiles acutipennis</i>	R	3	6	Baicich and Harrison (1997)
Cathartidae				
<i>Vultur gryphus</i>	R	5	6	Adams (1907); del Hoyo et al. (1994); Lambertucci and Mastrantuoni (2008)
Charadriiformes				
<i>Anous minutus marcusii</i>	R	1/7	4/5	Cullen and Ashmole (1963)
<i>Anous stolidus pileatus</i>	R	1/7	4/5	Pizzey (1980)
<i>Burhinus oedicnemus</i>	R	3	5/6	Harrison (1975)
<i>Charadrius alexandrinus</i>	R	3	6	Harrison (1975)
<i>Charadrius vociferus</i>	R	3	6	Baicich and Harrison (1997)
<i>Chlidonias leucopterus</i>	R	8	5	Harrison (1975)
<i>Chlidonias niger</i>	H	3/8	5/6	Bent (1963); Bergman et al. (1970); Harrison (1975)
<i>Fratercula arctica</i>	R	5	5	Harrison (1975)
<i>Fratercula cirrhata</i>	R	5	5	Baicich and Harrison (1997)
<i>Gelochelidon nilotica</i>	R	3	6	Baicich and Harrison (1997)
<i>Glareola pratincola</i>	R	3	6	Harrison (1975)

<i>Gygis alba</i>	R	1	6	Niethammer and Patrich-Castilaw (1998); Vanderwerf (2003)
<i>Haematopus ostralegus</i>	R	3	5	Harrison (1975)
<i>Himantopus mexicanus</i>	R	2/3	5/6	Baicich and Harrison (1997)
<i>Larus argentatus</i>	R	3/7	5	Harrison (1975)
<i>Larus atricilla</i>	R	3	5	Vleck et al. (1983); Baicichi and Harrison (1997)
<i>Larus canus</i>	R	3	5	Harrison (1975); Burger and Gochfeld (1987)
<i>Larus fuscus</i>	R	3	5	Harrison (1975)
<i>Larus glaucescens</i>	R	7	5	Baicich and Harrison (1997)
<i>Larus heermanni</i>	R	3/5	5	Baicich and Harrison (1997)
<i>Larus livens</i>	R	3/7	5	Baicich and Harrison (1997)
<i>Larus marinus</i>	R	3	5	Harrison (1975)
<i>Larus modestus</i>	R	3	6	Goodall et al. (1945)
<i>Larus ridibundus</i>	R	3/8	5/6	Harrison (1975)
<i>Larus serranus</i>	R	3/8	5	Burger and Gochfeld (1985); Carey et al. (1987)
<i>Limosa limosa</i>	R	3	5	del Hoyo et al. (1996); Baicichi and Harrison (1997)
<i>Numenius arquata</i>	R	3	5	Baicichi and Harrison (1997)
<i>Numenius phaeopus</i>	R	3	5	Harrison (1975)
<i>Onychoprion fuscatus</i>	R	3	6	Baicich and Harrison (1997)
<i>Onychoprion lunatus</i>	R	3	6	Whittow et al. (1985)

<i>Philomachus pugnax</i>	R	3	5	del Hoyo et al. (1996); Baicichi and Harrison (1997)
<i>Pluvialis apricaria</i>	R	3	5/6	Harrison (1975)
<i>Pluvianus aegyptius</i>	R	3	6	Howell (1979)
<i>Ptychoramphus aleuticus</i>	R	5	8	Baicich and Harrison (1997)
<i>Recurvirostra americana</i>	R	3	6	Baicich and Harrison (1997)
<i>Rissa tridactyla</i>	R	7	5	Baicich and Harrison (1997); Harrison (1975)
<i>Rynchops niger</i>	R	3	6	Baicich and Harrison (1997)
<i>Stercorarius maccormicki</i>	R	3	5/6	Watson (1975); Eppley (1996)
<i>Stercorarius skua</i>	R	3	5	Harrison (1975)
<i>Sterna forsteri</i>	R	3/8	5/6	Rockwell (1911); Godfrey (1966); Semenchuk (1993); Baicichi and Harrison (1997)
<i>Sterna hirundo</i>	R	3/8	5	Harrison (1975)
<i>Sterna paradisaea</i>	R	3	5/6	Harrison (1975)
<i>Sternula albifrons</i>	R	3	5	Harrison (1975)
<i>Thalasseus elegans</i>	R	3	6	Baicich and Harrison (1997)
<i>Thalasseus maximus</i>	R	3	6	Baicich and Harrison (1997)
<i>Thalasseus sandvicensis</i>	R	3	5/6	Harrison (1975)
<i>Tringa totanus</i>	R	3	5	del Hoyo et al. (1996); Baicichi and Harrison (1997)
<i>Uria aalge</i>	R	3/7	6	Harrison (1975)
<i>Uria lomvia</i>	R	7	6	Harrison (1975)

<i>Vanellus vanellus</i>	R	3	5	del Hoyo et al. (1996); Baicichi and Harrison (1997)
Ciconiiformes				
<i>Ardea albus</i>	R	1	4	Baicich and Harrison (1997)
<i>Bubulcus ibis</i>	R	1	4	Harrison (1975); del Hoyo et al. (1992)
<i>Egretta caerulea</i>	R	1	5	Ehrlich et al. (1988); Baicichi and Harrison (1997)
<i>Egretta garzetta</i>	R	1	4	Harrison (1975); del Hoyo et al. (1992)
<i>Egretta thula</i>	R	1	4	Baicich and Harrison (1997)
<i>Egretta tricolor</i>	R	1	4	Baicich and Harrison (1997)
<i>Eudocimus albus</i>	R	1/2/3	4	Baicich and Harrison (1997)
<i>Nycticorax nycticorax</i>	R	1/2	4	Harrison (1975)
<i>Plegadis falcinellus</i>	R	1/2/3	4/5	Harrison (1975)
<i>Plegadis ridgwayi</i>	R	3/8	5	Carey et al. (1987)
Columbiformes				
<i>Columba livia</i>	R	6/7	5	Harrison (1975)
<i>Streptopelia decaocto</i>	R	4	4	Harrison (1975)
<i>Streptopelia roseogrisea</i>	R	4	4	Goodwin (1967); del Hoyo et al. (1997)
<i>Streptopelia senegalensis</i>	R	1/7	4/5	Harrison (1975)
<i>Streptopelia turtur</i>	R	1	4	Harrison (1975)
<i>Zenaida macroura</i>	R	1/2	4	Baicichi and Harrison (1997)
Coraciiformes				

<i>Merops ornatus</i>	R	5	8	Lill and Fell (2007)
Falconidae				
<i>Falco naumanni</i>	R	4/5	6	Harrison (1975); del Hoyo et al. (1994); Snow and Perrins (1998)
<i>Falco tinnunculus</i>	R	4/7	5	Harrison (1975); Snow and Perrins (1998)
Galliformes				
<i>Alectoris graeca</i>	R	3/5	5	Harrison (1975)
<i>Alectura lathamii</i>	H	3	7	Pizzey (1980)
<i>Ammoperdix heyi</i>	R	3	6	Harrison (1975); Snow and Perrins (1998)
<i>Bonasa umbellus togata</i>	R	3	5	Baicich and Harrison (1997)
<i>Chrysolophus amherstiae</i>	R	3	5	Beebe (1931); del Hoyo et al. (1994)
<i>Chrysolophus pictus</i>	R	3	5/6	Goodwin (1948); del Hoyo et al. (1994); Snow and Perrins (1998)
<i>Coturnix coturnix</i>	R	3	5	Harrison (1975)
<i>Falcipennis canadensis canace</i>	R	3	5	Baicich and Harrison (1997)
<i>Gallus gallus</i>	R	3/4	5	Pizzey (1980)
<i>Gallus g. bankiva</i>	R	3/4	5	del Hoyo et al. (1994)
<i>Lagopus lagopus</i>	R	3	5	Steen et al. (1988); Hannon et al. (1998)
<i>Lagopus leucura</i>	R	3	5	Braun et al. (1993)
<i>Leipoa ocellata</i>	H	3	7	Pizzey (1980)

<i>Lophophorus impejanus</i>	R	3	5	Beebe (1931)
<i>Lophura nycthemera</i>	R	3	5	Harrison (1975)
<i>Lophura swinhoii</i>	R	3	5/6	Delacour (1951); del Hoyo et al. (1994)
<i>Meleagris gallopavo</i>	R	3	5	Harrison (1975); del Hoyo et al. (1994)
<i>Numida meleagris galeatus</i>	R	3	5	del Hoyo et al. (1994); Baicichi and Harrison (1997)
<i>Pavo cristatus</i>	R	3	5	Whistler (1949); del Hoyo et al. (1994)
<i>Pavo muticus</i>	R	3	5	Beebe (1931); del Hoyo et al. (1994); BirdLife International (2001)
<i>Phasianus colchicus</i>	R	3	5	Harrison (1975)
<i>Syrnaticus soemmerringii</i>	R	3	5	Yamashina (1961)
Gaviiformes				
<i>Gavia immer</i>	H	3/8	5	Vermeer (1973); Baicich and Harrison (1997)
Gruiformes				
<i>Fulica americana</i>	R	8	5	Gullion (1954); Carey et al. (1989a); Brisbin et al. (2002)
<i>Fulica atra</i>	R	3/8	5	Harrison (1975); Lomholt (1976); Fasola and Ruiz (1996)
<i>Gallinula tenebrosa</i>	R	3/8	5	Lill (1990); Taylor (1998)
<i>Porphyrio porphyrio</i>	R	8	5	Lill (1990); Taylor (1998)
Passeriformes				

<i>Agelaius phoeniceus</i>	R	1/2	1	Baicich and Harrison (1997)
<i>Carduelis tristis</i>	R	1/2	1	Baicich and Harrison (1997)
<i>Cercotrichas galactotes</i>	R	1	1	Harrison (1975)
<i>Cinnyris osea</i>	R	1	2	Harrison (1975); Paz (1987)
<i>Dendroica petechia</i>	R	1	1	Baicich and Harrison (1997); Rohwer and Law (2010)
<i>Ficedula hypoleuca</i>	R	4/5	1	Harrison (1975)
<i>Galerida cristata</i>	R	3	5	Harrison (1975); del Hoyo et al. (2004)
<i>Hippolais rama</i>	R	1	2	Hume (1889); del Hoyo et al. (1992); Castell and Kirwan (2005)
<i>Hirundo rustica</i>	R	6	1	Harrison (1975)
<i>Junco hyemalis</i>	R	1/3/5	1	Conway (1998); Nolan et al. (2002)
<i>Menura novaehollandiae</i>	R	3/4/5	2	Lill (1979); Pizzey (1980)
<i>Molothrus ater</i>	R	1	1	Baicich and Harrison (1997)
<i>Muscicapa striata</i>	R	4/5/6/7	1	Harrison (1975)
<i>Passer ammodendri</i>	R	4	2	del Hoyo et al. (1992)
<i>Passer domesticus</i>	R	4/5	2	Harrison (1975)
<i>Passer moabiticus</i>	R	1	2	Harrison (1975)
<i>Pica pica</i>	R	1	1	Baicichi and Harrison (1997)
<i>Ploceus capensis</i>	R	1	3	Brown (1994)
<i>Ploceus cucullatus</i>	R	1	3	Serle and Morel (1977)

<i>Prinia gracilis</i>	R	2	2	Harrison (1975)
<i>Pycnonotus capensis</i>	R	1	1	McLachlan and Liversidge (1970)
<i>Quiscalus quiscula</i>	R	1/4/7	1	Baicich and Harrison (1997)
<i>Riparia riparia</i>	R	5	8	Harrison (1975)
<i>Scotocerca inquieta</i>	R	2	3	Harrison (1975)
<i>Serinus canaria</i>	R	1	1	Harrison (1975)
<i>Sylvia curruca</i>	R	1	1	Harrison (1975); Flint et al. (1984)
<i>Sylvia mystacea</i>	R	1/2	1	Harrison (1975); Flint et al. (1984)
<i>Tachycineta bicolor</i>	R	4/5	1	Ehrlich et al. (1988); Robertson et al. (1992)
<i>Taeniopygia guttata</i>	R	1	2	Pizzey (1980)
<i>Troglodytes aedon</i>	R	4/5	1	Baicich and Harrison (1997)
<i>Turdus merula</i>	R	1/4/5	1	Harrison (1975)
<i>Turdus migratorius</i>	R	1/3/7	1	Baicich and Harrison (1997)
<i>Vermivora celata</i>	R	3	1	Sogge et al. (1994); Conway (1998)
<i>Vermivora virginiae</i>	R	3	1	Conway (1998); Olson and Martin (1999)
<i>Xanthocephalus xanthocephalus</i>	R	1/2	1	Baicichi and Harrison (1997)
Pelecaniformes				
<i>Anhinga anhinga</i>	R	1	4	Harrison (1975)
<i>Fregata minor</i>	R	1	4	Pizzey (1980)
<i>Phalacrocorax auritus</i>	R	1/7	4	Baicich and Harrison (1997)

<i>Phalacrocorax pelagicus</i>	R	7	5	Baicich and Harrison (1997)
<i>Sula leucogaster</i>	R	3/7	5/6	Pizzey (1980)
<i>Sula sula</i>	R	1/3	4/5	Pizzey (1980)
Phaethontidae				
<i>Phaethon rubricauda</i>	R	3/5	6	Pizzey (1980)
Phoenicopteriformes				
<i>Phoenicopus andinus</i>	R	3	6	del Hoyo et al. (1992)
Piciformes				
<i>Dendrocopos syriacus</i>	R	4	6	Harrison (1975)
Podicipediformes				
<i>Aechmophorus occidentalis</i>	H	8	5	Roberts (1936); Terres (1980); Baicich and Harrison (1997)
<i>Podiceps cristatus</i>	H	8	5	Harrison (1975); Lomholt (1976)
<i>Podiceps nigricollis</i>	H	8	5	Sotherland et al. (1984); Cullen et al. (1999)
<i>Podilymbus podiceps</i>	H	8	5	Roberts (1936); Ackerman and Platter-Rieger (1979); Davis et al. (1984); Ar and Rahn (1985); Baicich and Harrison (1997)
Procellariiformes				
<i>Bulweria bulwerii</i>	R	3/5	6	Harrison (1975)
<i>Fulmarus glacialis</i>	R	7	6	Harrison (1975)

<i>Oceanodroma furcata</i>	R	3/5	5/8	Baicich and Harrison (1997)
<i>Oceanodroma leucorhoa</i>	R	4/5	5/8	Harrison (1975)
<i>Phoebastria immutabilis</i>	R	3	5	Dill (1916)
<i>Phoebastria nigripes</i>	R	3	5	Richards (1909); Whittow (1993)
<i>Pterodroma hypoleuca</i>	R	5	8	Howell and Bartholomew (1961)
<i>Pterodroma phaeopygia</i>	R	5	8	Harris (1970)
<i>Puffinus pacificus</i>	R	3	8	Howell and Bartholomew (1961); Whittow (1997)
<i>Puffinus tenuirostris</i>	R	5	8	Bradley et al. (2000)
Psittaciformes				
<i>Agapornis personatus</i>	R	4	2	Mackworth-Praed and Grant (1957); del Hoyo et al. (1997); Hansell (2000)
<i>Agapornis roseicollis</i>	R	5	1	McLachlan and Liversidge (1970); del Hoyo et al. (1997)
<i>Bolborhynchus lineola</i>	R	4/5	4*	Hilty and Brown (1986); del Hoyo et al. (1997); Krabbe et al. (2009)
<i>Enicognathus ferrugineus</i>	R	4	4	Johnson (1967); del Hoyo et al. (1997)
<i>Melopsittacus undulatus</i>	R	4/5	4	Baicich and Harrison (1997)
Pteroclididae				
<i>Pterocles namaqua</i>	R	3	6	del Hoyo et al. (1997)
<i>Pterocles orientalis</i>	R	3	6	Harrison (1975); Hinsley et al (1993); Znari et al. (2008)

Sphenisciformes				
<i>Aptenodytes patagonicus</i>	R	9	9	Handrich (1989)
<i>Pygoscelis adeliae</i>	R	3	6	Goodfellow (1977)
<i>Spheniscus demersus</i>	R	3	5	Seddon and van Heezik (1991); Kemper et al. (2007)
Strigiformes				
<i>Bubo bubo</i>	R	4/5	6	Harrison (1975)
<i>Strix aluco</i>	R	3/4/5/7	6	Harrison (1975)
<i>Tyto alba</i>	R	4/5	6	Harrison (1975)
Struthioniformes				
<i>Apteryx australis</i>	R	4/5	5	Calder III (1979); Colbourne (2002)
<i>Dromaius novaehollandiae</i>	R	3	5	Pizzey (1980); del Hoyo et al. (1992)
<i>Rhea americana</i>	R	3	5	Fernandez and Reboreda (1995); Davies (2002)
<i>Rhea pennata</i>	R	3	5	del Hoyo et al. (1992)
<i>Struthio camelus</i>	R	3	6	Goodfellow (1977); Serle and Morel (1977); Davies (2002)
Tinamiformes				
<i>Eudromia elegans</i>	R	3	5	Mezquida (2001); Davies (2002)