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Sexual monomorphism in wing loading and wing aspect ratio in Black Vulture (*Coragyps atratus*) and Turkey Vulture (*Cathartes aura*)

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Abstract.—Sexual dimorphism patterns in wing area, wing loading, and wing aspect ratio of Black Vulture (*Coragyps atratus*) and Turkey Vulture (*Cathartes aura*) are unknown but are of particular interest given the prevalence of these species in scavenging communities in the Western Hemisphere. I assessed these variables in sexed specimens from wintering populations in Nashville, Tennessee. Black Vultures exhibited higher wing loading and a lower wing aspect ratio than Turkey Vultures. Neither species exhibited significant age-related or sexual dimorphism in body weight, wing span, wing area, wing loading, or wing aspect ratio. The relatively low variance observed in the pooled sample of immatures (~9–21 mo old) and adults suggests that definitive wing size and shape are acquired several years before individuals develop the bare rugose skin and head caruncles characteristic of adults. In a broader context, this study tentatively suggests that variance estimates for wing morphology obtained from unsexed vulture populations may not be unduly inflated by undetected sexual or age-related dimorphism.

Keywords: Cathartidae, sexual dimorphism, wing area, wing aspect ratio, wing loading, wing span.

New World vultures (Aves: Accipitriformes: Cathartidae) comprise a well-defined monophyletic clade (Johnson et al. 2016) distantly related to the Accipitriform raptors (Jarvis et al. 2014, Prum et al. 2015). Sexual size dimorphism, the difference between females and males in mean body size, varies greatly in diurnal raptors (Storer 1966, Snyder & Wiley 1976, Blake 1977, Cramp & Simmons 1980, Anderson & Norberg 1981). Most species exhibit female-biased size dimorphism in which females are larger than males (Storer 1966, Snyder & Wiley 1976, Blake 1977, Cramp & Simmons 1980, Anderson & Norberg 1981). Nearly two dozen hypotheses have been proposed for the evolution of female-biased size dimorphism in raptorial birds (Earhart & Johnson 1970, Amadon 1975, Snyder & Wiley 1976, Anderson & Norberg 1981, Jehl & Murray 1986, Korpimäki 1986, Lundberg 1986, Mueller 1986, 1990, Hakkarainen & Korpimäki 1991, Bildstein 1992, Krüger 2005), the most likely of which involve the partitioning of nesting labor, prey size matching, prey agility, and nest defense (Andersson & Norberg 1981). Raptors that specialize on birds exhibit the greatest sexual dimorphism whereas those that prey on lethargic invertebrates, amphibians, and reptiles display the least dimorphism. Vultures

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are predicted to show the lowest levels of dimorphism because their prey is immobile.

The seven extant species of New World vultures exhibit a spectrum of size dimorphism ranging from subtle female-biased size dimorphism in Turkey Vulture (*Cathartes aura*), Lesser Yellow-headed Vulture (*Cathartes burrovianus*), and Greater Yellow-headed Vulture (*Cathartes melambrotus*), to monomorphism in King Vulture (*Sarcoramphus papa*) and Black Vulture (*Coragyps atratus*), and male-biased size dimorphism in California Condor (*Gymnogyps californianus*) and Andean Condor (*Vultur gryphus*) (Koford 1953, Wetmore 1964, Blake 1977, Palmer 1988). Size dimorphism estimations have been based largely on wing chord measurements of internally sexed museum specimens.

New World vultures are the preeminent avian scavengers in the Western Hemisphere and few other land birds depend so heavily on soaring flight to find food. Dominance hierarchies at carrion are believed to correlate with body mass and age (Wallace & Temple 1987, Kirk & Houston 1995, Sheppard et al. 2013), but the relationship of sexual size dimorphism to vulture foraging ecology, dominance hierarchies at feeding and roosting assemblages, and courtship behavior is poorly understood in condors (Wallace & Temple 1987, Sheppard et al. 2013) and unknown in the remaining species (Wallace & Temple 1987, Houston 1988, Kirk & Houston 1995, Buckley 1996).

Patterns of sexual size dimorphism in Black and Turkey vultures are of particular interest because of their prevalence in scavenging communities from Canada to Tierra del Fuego (Rabenold 1987, Houston 1988, Kirk & Gosler 1994, Buckley 1997, Carrete et al. 2010, Shepard & Lambertucci 2013, Grilli et al. 2017). Wing morphology has been addressed in several studies of Black Vulture but surprisingly little data have been obtained from individuals of known sex (Raspet 1960, Parrott 1970, Pennycuick 1983, Houston 1988, Kirk & Gosler 1994, Shepard & Lambertucci 2013). Raspet (1960) and Parrott (1970) obtained wing measurements from a single unsexed individual and Pennycuick (1983) made rough wing measurements of two females from Panama. The latter reference includes the sole measurements of wing area of known-sex individuals. Houston (1988) communicated measurements of wing span, wing area, wing loading and wing aspect ratio for a moderate number of unsexed Black and Turkey vultures, but did not source the data methods or the populations sampled. Kirk and Gosler (1994) measured wing span, wing width, and body mass, but not wing area, in a large sample of unsexed Black Vultures in Venezuela. Recently, Shepard and Lambertucci (2013) measured wing area and wing loading for a population sample of unsexed individuals in Argentina.

Published reports of wing area for Turkey Vultures appear to be limited to four reports of unsexed individuals (Poole 1938, Houston 1988, Kirk & Gosler 1994, Grilli et al. 2017). Poole (1938) reported wing area and body mass, but not wingspan, for a single individual. Houston (1988) communicated wing morphology data from unsexed individuals from an unknown locality. Kirk and Gosler (1994) measured wing span, wing width, and body mass, but not wing area, for a large sample of resident and migratory populations in Venezuela. Finally, Grilli et al. (2017) measured wingspan, wing area, body mass, and aspect ratio for populations from Arizona, Saskatchewan, Pennsylvania, Argentina, and the Falkland Islands. In total, wing morphology of several hundred Turkey Vultures has been measured in the field but none of the birds were sexed.

Here I investigate sexual and age-related patterns of variation in wing span, wing area, wing loading, and wing aspect ratio for sexed individuals of Black and Turkey vultures wintering in Nashville, Tennessee. I asked two basic questions: (*i*) Does wing morphology of yearlings (~9–21 months old) differ from that of older age classes? (*ii*) Are wing variables sexually dimorphic?

Methods

Black Vultures ($n = 26$) and Turkey Vultures ($n = 23$) were salvaged from 13 to 17 February 2012 during scheduled population control activities conducted by APHIS Wildlife Services (United States Department of Agriculture), under the authority of the US Fish & Wildlife Service, in the vicinity of Nashville, Tennessee (36°10.6′N, 86°46.8′W). Our primary objective was to obtain specimens for studies of the gastrointestinal microbiome (Roggenbuck et al. 2014), sensory anatomy (Lisney et al. 2013), and facial integument (Graves 2016). Black Vultures in eastern North America represent the large northern subspecies, *Coragyps a. atratus* (Blake 1977, Palmer 1988, Buckley 1999). This population is largely non-migratory although some individuals withdraw from the northern portion of the breeding range in winter (Buckley 1999). Wintering Turkey Vultures in Tennessee represent the widespread eastern subspecies, *Cathartes aura septentrionalis* (Wetmore 1964). The Nashville sample was likely composed of local breeding birds but may include wintering individuals from north-central United States and Ontario (Kirk & Mossman 1998)

Measurements.—Individuals were weighed to the nearest 5 g on a digital scale. Following recent discussions in the literature, I use weight rather than mass to describe the measurements (Lidicker 2008). Most stomachs were empty or contained little food. Qualitative fat levels were recorded for 23 of 26 Black Vultures and 22 of 23 Turkey Vultures at necropsy. Fat levels were "very heavy" or "extremely heavy" in the vast majority of individuals (Black Vulture: 82% of females and 100% of males. Turkey Vulture: 93% of females and 100% of males). This suggests that carrion was abundant in the Nashville area (see Roggenbuck et al. 2014). Although Black and Turkey vultures may initiate breeding as early as March in Tennessee, none of the vultures obtained in February were in breeding condition (largest ova <10 mm in diameter; greatest testis length <20 mm). To measure wingspan (Baldwin et al. 1931), dead birds were placed on their backs on an examination table. Wings in light rigor were loosened up with repetitive flexing before measurement. Wings were fully spread by two or three people without deforming the natural curvature of the outer primaries. Wingspan was measured (nearest cm) from the ventral side with a flexible measuring tape placed across the ventral side of the neck.

Whole wings were detached from the body at the proximal humeral joint. Major wing muscles were removed before the wings were prepared in a spread position with intact wing bones and fully fanned primaries (Fig. 1). Ligamentous attachments of the flight feathers to wing bones were not disturbed. Voucher specimens were deposited in the research collections of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. Wing area (nearest cm^2) and greatest wing width (leading edge of the wing to the trailing edge) were measured from standardized photographs of dried spread wings with the histogram tool in Adobe Photoshop version CS5. Four specimens (8%) had 1–3 missing primary tips (shot off). I digitally replaced the missing feather tips with Abobe Photoshop before calculating wing area. Wing area (Table 1) is defined as the area of both wings plus the rootbox, the part of the body between the wings (Pennycuick 2008). Vultures are supported in gliding flight by a zone of reduced air pressure that extends from one wing tip to the other

Fig. 1. Spread wings of Black Vulture (top) and Turkey Vulture (bottom). Both examples exhibit the pointed primary tips and narrower more pointed primary wing coverts typical of immature birds.

across the back. The chord of the root box (leading to trailing edge) was equivalent to the greatest wing width. Wing aspect ratio was defined as the wing span squared divided by wing area (Pennycuick 2008). A low wing aspect ratio indicates relatively short and broad wings whereas a high aspect ratio indicates long and narrow wings.

Age determination.—Definitive plumage and skin characters are acquired 3–4 yr after fledging in Black and Turkey vultures (Palmer 1988, Pyle 2005). Specimen age for both species in the Nashville population sample ranged from yearlings (a minimum of 9 mo old), with a bursa of Fabricius (Glick 1983) and dense filoplumes on the head and neck, to older adults with definitive soft part colors and head feathering. Although it might be possible to distinguish three age classes on the basis of plumage (Pyle 2005), an unequivocal benchmark occurs when the sharply pointed outer primaries (especially P10) of immatures are replaced by more rounded primaries during the second year after hatching (a minimum of 21 mo old). Wing size and shape are likely stable after the secondaries and primaries have been replaced at least once. In this study, I

Table 1.—Minimum and maximum (mean ± standard deviation) values for body mass, wing span, wing area, wing loading, and wing aspect ratio of Black and Turkey vultures wintering in Nashville, Tennessee.

Species	Sex	Body mass (kg)	Wing span (m)	Wing area (m^2)[a]	Wing loading (kg/m^2)	Aspect ratio[b]
Black Vulture	Female ($n = 19$)	2.03–2.45 $\bar{X} = 2.20 \pm 0.11$	1.36–1.52 $\bar{X} = 1.44 \pm 0.04$	0.308–0.383 $\bar{X} = 0.350 \pm 0.017$	5.49–7.05 $\bar{X} = 6.29 \pm 0.40$	5.65–6.24 $\bar{X} = 5.94 \pm 0.17$
	Male ($n = 7$)	1.80–2.21 $\bar{X} = 2.04 \pm 0.13$	1.32–1.49 $\bar{X} = 1.44 \pm 0.06$	0.316–0.365 $\bar{X} = 0.348 \pm 0.018$	5.54–6.31 $\bar{X} = 5.85 \pm 0.32$	5.53–6.14 $\bar{X} = 5.94 \pm 0.20$
Turkey Vulture	Female ($n = 15$)	2.02–2.57 $\bar{X} = 2.22 \pm 0.14$	1.70–1.80 $\bar{X} = 1.75 \pm 0.03$	0.419–0.502 $\bar{X} = 0.461 \pm 0.023$	4.46–5.24 $\bar{X} = 4.82 \pm 0.22$	6.43–6.94 $\bar{X} = 6.65 \pm 0.17$
	Male ($n = 8$)	1.86–2.37 $\bar{X} = 2.06 \pm 0.16$	1.67–1.80 $\bar{X} = 1.72 \pm 0.04$	0.424–0.476 $\bar{X} = 0.444 \pm 0.017$	4.12–5.27 $\bar{X} = 4.63 \pm 0.33$	6.45–7.00 $\bar{X} = 6.67 \pm 0.18$

[a] area of both wings + root box.
[b] (wing span × wing span)/wing area.

differentiated age classes on the basis of primary shape—pointed in immature specimens and rounded in adults. Sample bins for sex classes within sex and species were relatively small and provide only modest statistical power to tease out age-related variation in wing morphology (Black Vulture: adult ♀♀ = 11; immature ♀♀ = 8; adult ♂♂ = 2; immature ♂♂ = 5. Turkey Vultures: adult ♀♀ = 10; immature ♀♀ = 5; adult ♂♂ = 6; immature ♂♂ = 2).

Statistics.—I used general linear models (SYSTAT version 12) to investigate the effects of categorical variables (sex and age class) and on body weight, wing span, wing area, wing loading, and wing aspect ratio of Black and Turkey vultures (Appendix 1). I used a conservative Bonferroni correction to control familywise error rate. Alpha ($\alpha = 0.05$) was adjusted for the number of simultaneously generated *P*-values ($\alpha = 0.05/30 = 0.002$). The relationship between wing loading and aspect ratio was explored with a bivariate scatterplot.

Results and Discussion

Wing loading and wing aspect ratio affect soaring efficiency, air speed, climb rates, circling diameter, and take-off from level surfaces of vultures and other large birds (Rayner 1988, Pennycuick 2008). It has long been known that Black Vultures have significantly higher wing loading and lower aspect ratios than Turkey Vultures (Fisher 1946, Stager 1964, Houston 1988, Kirk & Gosler 1994) but the degree of difference in sympatric populations of the two species has not been explicitly addressed. Black and Turkey vultures wintering in the Nashville area occupy discreet areas in bivariate space for wing aspect ratio and wing loading data (Fig. 2). Both species have slotted wing tips conducive to soaring but the higher aspect ratio and lower wing loading of Turkey Vultures facilitate slower flight speeds and permit them to exploit smaller updrafts closer to

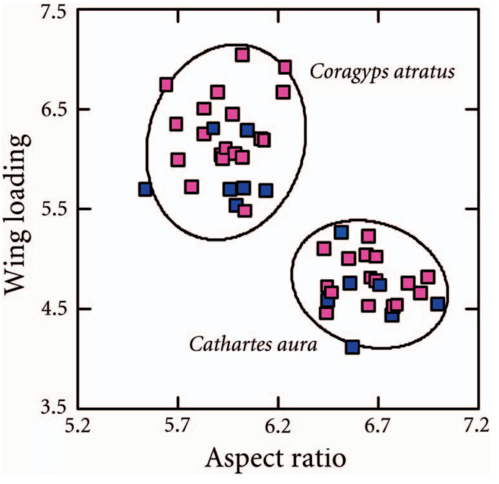

Fig. 2. Bivariate plot of wing loading (kg/m^2) and wing aspect ratio (wing span squared/wing area) for Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) wintering in Nashville, Tennessee. Confidence ellipses (0.9) surround data points for each species (♀♀ = magenta, ♂♂ = blue).

the forest canopy whereas the lower wing aspect ratio of Black Vulture appears to facilitate quicker take-offs from the ground (Pennycuick 1983, Houston 1988, Palmer 1988, Kirk & Houston 1995).

When statistical tests were adjusted for familywise error rate, none of the variables exhibited significant sexual dimorphism or age-related variation (Appendix 1). The distribution of data points for males and females overlaps broadly within the confidence ellipses for each species in the bivariate plot for wing aspect ratio and wing loading (Fig. 2). The relatively low variance observed in morphological variables (Table 1, Fig. 2) in the pooled data, composed of immatures (~9–21 mo old) and adults, suggests that definitive wing size and shape are acquired several years before individuals fully develop the bare rugose neck skin and head caruncles characteristic of adults. In a broader context, this study tentatively suggests that variance estimates for wing morphology of Black and Turkey vultures obtained from individuals of undetermined sex (Kirk & Gosler 1994, Grilli et al. 2017) may not be unduly inflated by undetected sexual dimorphism.

The only comparable dataset was published recently by Grilli et al. (2017). Unsexed Turkey Vultures from Pennsylvania (Grilli et al. 2017) had significantly lower body weight ($P < 0.001$), shorter wing span ($P < 0.001$), smaller wing area ($P < 0.001$), and lower wing loading ($P < 0.002$) than the pooled sample of males and females reported in this study from Tennessee. In contrast, wing aspect ratios of Pennsylvania and Tennessee populations did not differ ($P = 0.38$), which is consistent with the finding of Grilli et al. (2017) that Turkey Vulture populations from Pennsylvania, Arizona, Saskatchewan, Argentina, and the Falkland Islands had similar wing aspect ratios but different wing loadings (Grilli et al. 2017).

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Appendix 1.—General linear model for sex and age class effects on morphological variables of Black and Turkey vultures wintering in Nashville, Tennessee. Significance level was adjusted for the number of simultaneously generated *P*-values ($\alpha = 0.05/30 = 0.002$).

Source	Type III SS	df	Mean squares	*F*-ratio	*P*-value
Dependent variable: Body weight					
Black Vulture ($r^2 = 0.37$)					
Sex	0.06	1	0.06	4.88	0.04
Age	0.03	1	0.03	2.67	0.11
Sex × Age	0.03	1	0.03	2.33	0.14
Error	0.28	22	0.01		
Turkey Vulture ($r^2 = 0.44$)					
Sex	0.16	1	0.16	9.05	0.01
Age	0.12	1	0.12	6.75	0.02
Sex × Age	0.01	1	0.01	0.34	0.56
Error	0.33	19	0.02		
Dependent variable: Wing span					
Black Vulture ($r^2 = 0.07$)					
Sex	0.00	1	0.00	0.01	0.91
Age	0.00	1	0.00	0.08	0.78
Sex × Age	0.00	1	0.00	0.80	0.38
Error	0.05	22	0.00		
Turkey Vulture ($r^2 = 0.32$)					
Sex	0.01	1	0.01	2.21	0.15
Age	0.00	1	0.00	0.83	0.37
Sex × Age	0.00	1	0.00	1.66	0.21
Error	0.02	19	0.00		
Dependent variable: Wing area					
Black Vulture ($r^2 = 0.11$)					
Sex	<0.01	1	<0.01	0.04	0.84
Age	<0.01	1	<0.01	0.07	0.80
Sex × Age	<0.01	1	<0.01	1.61	0.22
Error	0.01	22	<0.01		
Turkey Vulture ($r^2 = 0.43$)					
Sex	<0.01	1	<0.01	2.28	0.15
Age	<0.01	1	<0.01	4.42	0.05
Sex × Age	<0.01	1	<0.01	1.74	0.20
Error	0.01	19	<0.01		
Dependent variable: Wing loading					
Black Vulture ($r^2 = 0.40$)					
Sex	0.45	1	0.45	3.67	0.07
Age	0.19	1	0.19	1.53	0.23
Sex × Age	0.80	1	0.80	6.47	0.02
Error	1.26	22	0.12		
Turkey Vulture ($r^2 = 0.25$)					
Sex	0.35	1	0.35	5.26	0.03
Age	0.13	1	0.13	1.91	0.18
Sex × Age	0.19	1	0.19	2.82	0.11
Error	1.26	19	0.07		

Appendix 1.—Continued.

Source	Type III SS	df	Mean squares	*F*-ratio	*P*-value
Dependent variable: Wing aspect ratio					
Black Vulture ($r^2 < 0.01$)					
Sex	<0.01	1	<0.01	<0.01	0.96
Age	<0.01	1	<0.01	0.02	0.89
Sex × Age	<0.01	1	<0.01	0.03	0.85
Error	0.75	22	0.03		
Turkey Vulture ($r^2 = 0.25$)					
Sex	<0.01	1	<0.01	0.08	0.78
Age	0.12	1	0.12	5.03	0.04
Sex × Age	<0.01	1	<0.01	0.05	0.82
Error	0.46	19	0.02		