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WING LOADING IN NORTH AMERICAN GOLDEN EAGLES (AQUILA CHRYSAETOS)

JAMES W. LISH¹

Department of Physiological Sciences, Center for Veterinary Health Sciences, Oklahoma State University, Stillwater, OK 74078 U.S.A.

> ROBERT DOMENECH Raptor View Research Institute, P.O. Box 4323, Missoula, MT 59806 U.S.A.

> > BRYAN E. BEDROSIAN

Craighead Beringia South, P.O. Box 147, Kelly, WY 83011 U.S.A.

DAVID H. ELLIS

Institute for Raptor Studies, 3722 East Defiance Street, Oracle, AZ 85623 U.S.A.

MARK PAYTON

Department of Statistics, Oklahoma State University, Stillwater, OK 74078 U.S.A.

ABSTRACT.—We present wing-loading measurements for 33 Golden Eagles (*Aquila chrysaetos*) trapped during autumn migration in Montana and Wyoming, and we compare wing loading and other related variables between age classes (hatch-year and adult) and sexes. Adult females had significantly greater wing loading than hatch-year females and both adult and hatch-year males. Adult and hatch-year males had similar wing loading. Hatch-year females weighed less than adult females, whereas the mass of hatch-year and adult males did not differ. Although our sample of wing-loading estimates for 33 Golden Eagles is small, it is the largest currently available for this species and this manuscript is the first to present age- and sex-specific comparisons of this important flight parameter. Our study distinguishes interesting and previously unidentified differences in mass and wing loading between sex and age categories, which may have important implications for energetics during foraging and migration, and merit further investigation.

KEY WORDS: Golden Eagle; Aquila chrysaetos; mass; morphometrics; wing loading; wingspan.

CARGA ALAR DE INDIVIDUOS NORTEAMERICANOS DE AQUILA CHRYSAETOS

RESUMEN.—Presentamos las medidas de carga alar de 33 individuos de *Aquila chrysaetos* atrapados en Montana y Wyoming durante la migración otoñal y comparamos la carga alar y otras variables relacionadas entre las clases de edad (aves del primer año y adultos) y los sexos. Las hembras adultas presentaron una carga alar significativamente mayor que la de las hembras del primer año y que la de los machos adultos y del primer año. Los individuos machos adultos y del primer año tuvieron cargas alares similares. Las hembras del primer año pesaron menos que las hembras adultas, mientras que la masa de los machos adultos y del primer año no difirió. Aunque nuestra muestra de estimaciones de cargas alares para 33 individuos de *A. chrysaetos* es pequeña, es la más grande disponible actualmente para esta especie y este manuscrito es el primero en presentar comparaciones específicas para la edad y el sexo de este importante parámetro de vuelo. Nuestro estudio distingue diferencias interesantes y que no fueron identificadas previamente en cuanto a la masa y la carga alar entre las categorías de edad y de sexo, las que pueden tener importantes implicancias energéticas durante la búsqueda de comida y la migración, lo que amerita mayor investigación.

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¹Email address: jim.lish@okstate.edu

Wing loading is the ratio of a bird's mass to the surface area of its wings (Brown and Amadon 1968), typically expressed in units of g/cm² (Clark 1971). As wing loading increases, higher flight speeds, and thus greater energy expenditures, are required to produce lift (Podulka and Rohrbaugh 2004). The wing loading of birds of prey affects how fast they can rise in thermals and their minimum and maximum flight speeds, gliding efficiency, and turning radii, which in turn influence the energetics of maneuvering in different habitats, prey choice and capture, and migration (Brown and Amadon 1968, Brown 1976, Cade 1982, Mueller et al. 1981, 2002, 2004).

Relatively few studies have quantified the wing loading of Accipitriformes, with sex- and age-specific comparisons especially limited (Mueller et al. 1981). Mueller et al. (1981, 2002, 2004) investigated the wing loading of Sharp-shinned Hawks (*Accipiter striatus*), Merlins (*Falco columbarius*), and Red-tailed Hawks (*Buteo jamaicensis*); however, no detailed investigations of wing loading have been published for members of the genus *Aquila*. For Golden Eagles (*Aquila chrysaetos*), we found published estimates of wing loading for only two individuals, with no information provided about the sex or age of the eagles or methods used to derive the estimates (Poole 1938, Brown and Amadon 1968).

We present wing-loading measurements for 33 Golden Eagles captured during autumn migration in Montana and Wyoming from 2007–2013, and compare differences between the sexes and between hatch-year and adult eagles. We also discuss methods for measuring wing area for these large birds under field conditions. Ancillary to our main objective of measuring wing loading, we also examined the relationship between wing chord, a frequently taken ornithological measurement, and wing area, to determine if wing chord could be used to accurately estimate wing area in this species.

METHODS

We captured eagles using bow nets baited with live nonnative Rock Pigeons (*Columba livia*) and placed along known ridgeline migration routes. We also used net launchers (Trapping Innovations, LLC, Kelly, WY U.S.A.) baited with carrion placed in open areas at lower elevations. Evidence suggests that Golden Eagles in North America are predominately nonmigratory below approximately 55° north latitude (Kochert et al. 2002); however, juveniles from southern populations often disperse widely from their natal areas in autumn (Steenhof et al. 1984) and probably contribute to flight activity seen at migration watch sites (Hoffman and Smith 2003). Therefore, although evidence collected during a coincidental study of eagles at our trap sites (Domenech et al. 2015) suggested that most of the eagles captured for this study were northern migrants, we cannot be certain about the origins of the hatch-year birds.

We aged eagles using criteria presented by Bloom and Clark (2001), with the modifications proposed by Ellis (2004). The latest trapping date for hatchyear eagles was 28 October, well before the onset of first molt. We collected blood from the brachial vein of 27 of the 33 focal eagles for DNA-based sex identification (Zoogen DNA Services, Davis, CA U.S.A.). We determined the sex of the remaining six eagles using morphometrics (Bortolotti 1984, Edwards and Kochert 1986); all six eagles had unequivocal measurements (Harmata and Montopoli 2013).

We measured the mass of eagles using a Pesola hanging scale accurate to ± 100 g (Pesola AG, Switzerland). Four of the 33 focal eagles had palpable crop contents. For these individuals, we estimated the mass of crop contents based on available estimates of average full-crop mass (Harmata and Montopoli 2013), and reduced the measured eagle masses by those amounts. We measured unflattened wing chord as defined by Proctor and Lynch (1993), wing span as twice the length from the midline of the body at its greatest width to the distal tip of the furthermost extending primary of a fully extended wing, and wing length as the distance from the root line (the most proximal extent of the patagium and the proximal edge of the innermost secondary remiges; Pennycuick 1989) to the distal tip of the furthermost extending primary in a fully extended wing.

Estimates of wing surface areas are most useful when determined from wings held in the position at which the greatest power is generated, such as during the middle portion of the downstroke or, for large soaring birds like Golden Eagles, the position of the wing while ascending in a thermal (Stiles and Altshuler 2004). We estimated the surface area of a fully extended wing from a digital photograph of its ventral surface, taken with the wing held behind and slightly contacting a clear Plexiglas sheet marked with a grid of known dimensions (Fig. 1). The grid allowed us to accurately scale the image and check the degree of distortion in the photograph.



Figure 1. Photograph of a Golden Eagle wing extended behind a clear Plexiglas sheet and a 5.4-cm grid, with a tracing used to estimate the wing surface area indicated on the figure.

To calculate wing areas, we uploaded the images into Adobe® Photoshop® CS4 (Adobe Systems Incorporated, San Jose, CA U.S.A.), where we corrected distortion, removed glare, sharpened the image, and increased contrast for easier outlining. We calculated the surface area of the wing using Image I (National Institutes of Health, Bethesda, MD U.S.A.), then multiplied the single wing area by two to calculate wing loading. To ensure accurate comparisons among individuals, we filled gaps left by missing, molted, or broken feathers by outlining their estimated length and position. We truncated the wing outline at the root line. We determined sample error by outlining three different wings five times each. Variation within the three sets of estimated wing areas ranged from 0.2-0.3% of the mean. To further reduce error when calculating wing areas with Image I, we always set the scale using the maximum number of grid cells of known dimensions that were visible in the photograph.

We assessed differences in wing loading and other measurements among age and sex classes using twoway factorial analysis of variance (ANOVA). For each measurement, we assessed the simple effects of age given sex and sex given age with planned contrasts of the least square means within the ANOVA model. We considered $P \leq 0.05$ indicative of a significant difference. We also developed a simple linear regression model to study the feasibility of using wing chord to predict wing area.

RESULTS

For six metrics related to wing loading, the average values for adult females always exceeded those of adult males (P < 0.006; Table 1). Most notably, compared to adult males, adult females averaged 31% heavier (P < 0.001) and had 18% heavier wing loading (P < 0.006). Adult females were also heavier and had heavier wing loading than hatch-year females (P < 0.004). In contrast, hatch-year and adult males had similar wing loading (P = 0.52) and mass (P = 0.40). The only wing metric that differed between adult and hatch-year males was wing length; hatch-years averaged 4% longer wings (P < 0.030). Based on our dataset, wing chord was not a strong predictor of wing area ($r^2 = 0.64$; Fig. 2).

Because adults were heavier than hatch-year eagles among females but not males, we expanded our investigation of sex and age differences in mass to a larger dataset (n = 127 Golden Eagles captured at the same trapping site, all DNA-sexed and aged by the same criteria as our sample of 33 focal eagles) to help validate the indicators derived from the smaller sample. The ANOVA results based on the larger sample confirmed that adult females averaged heavier than hatch-year females (P < 0.001), but there was no difference between adult and hatch-year males (P = 0.63).

MEASUREMENT	ADULT σ n = 15	Hatch-year o' $n = 5$	ADULT Q $n = 6$	HATCH-YEAR Q $n = 7$
Mean mass (g) ±SD	3553.3 ± 238.4	3730.0 ± 417.7	5097.0 ± 564.1	4257.0 ± 531.8
Range	3250 - 4180	3250 - 4400	4600-6000	3600 - 5300
Mean wing chord (cm) \pm SD	58.7 ± 12.0	58.3 ± 13.0	63.2 ± 14.2	63.0 ± 20.4
Range	56.5 - 61.2	56.2 - 59.7	61.9 - 65.9	61.0-65.9
Mean wing length (cm) \pm SD	88.5 ± 3.0	92.0 ± 4.1	95.8 ± 2.9	95.4 ± 2.9
Range	83.0-93.5	87.4 - 98.0	91.9 - 98.8	90.9-99.0
Mean wing span (cm) \pm SD	192.8 ± 6.1	191.6 ± 4.5	212.2 ± 6.2	209.2 ± 9.1
Range	182.6 - 203.8	186.1 - 197.2	202.7 - 221.8	197.3 - 221.7
Mean wing area $(cm^2) \pm SD$	5028.5	5040.8	5879.2	5899.3
Range	4405.8 - 5577.3	4811.4-5225.5	5584.8 - 6186.3	5497.7 - 6281.7
Mean wing loading $(g/cm^2) \pm SD$	0.71 ± 0.08	0.73 ± 0.06	0.86 ± 0.09	0.72 ± 0.09
Range	0.60 - 0.88	0.67 - 0.84	0.77 – 0.98	0.64-0.90

Table 1. Wing morphometrics for 33 Golden Eagles captured during autumn migration in Montana and Wyoming.

DISCUSSION

Raptor researchers have defined wing area in various ways. Pennycuick (1989) defined wing area as the area of both wings plus the area projected by that part of the body between the wings, called the root box. Most other researchers have excluded the root box from estimates of wing area (Poole 1938, Brown and Amadon 1968, Cade 1982), as we have. As Brown and Amadon (1968) pointed out, "The flying surfaces of a bird of prey consist of the wings and tail, spread or closed. The body of a hawk is less important, though presumably on occasion it can provide additional lift." Researchers wishing to make between-study comparisons should consider that including or excluding the root box from estimates of wing area necessarily results in different estimates of wing loading. Calls for consistency in wingloading methodology and terminology have been proposed, but generally not heeded (Clark 1971), and because of this methodological variation, between-study comparisons of wing-loading estimates are currently problematic. Because of methodological variation and small or unreported sex-specific sample sizes for studies pertaining to the genus *Aquila*, we restricted our focus to withinstudy comparisons.

The adaptive advantages of reversed sexual size dimorphism in raptors have been discussed at length (e.g., Snyder and Wiley 1976, Andersson and Norberg 1981). The wing-loading differential between mates in Golden Eagle pairs likely widens their foraging niche, which is especially advantageous for raptors that hunt cooperatively (Kochert et al. 2002). Adult male Golden Eagles may benefit from lighter wing loading than females during the nesting season, when the male does most of the hunting and conserving energy is important for transporting prey from distant locations.

One of the surprising results of our study is that the wing surface areas of hatch-year and adult birds did not differ for either sex. We predicted that, within sexes, hatch-year birds would have greater



Figure 2. Relationship of wing chord and wing surface area for 33 Golden Eagles captured and measured during autumn migration in Montana and Wyoming.

wing surface areas than adults, because among Golden Eagles first-generation secondary remiges are 1-2 cm longer than older-generation secondaries. There are three possible explanations for why age-specific differences in wing surface area were not observable in this sample. First and most importantly, although our sample of 33 eagles is the largest available for a member of the genus Aquila, it is still small, thus limiting the statistical power of our analysis to detect differences. Second, the increase in wing area resulting from longer secondary remiges may be too small in relation to the overall wing-surface area of Golden Eagles to be detectable with the level of measuring precision we employed. Another possibility is that as the flight surfaces of the secondary remiges decrease with maturity, the flight surfaces of the primary remiges may increase. Because the primaries provide the majority of forward propulsion during flapping flight, it could be that, as strength and conditioning increase with maturity, adult birds are able to power larger primary surfaces for more thrust and speed.

In our sample of eagles, the hatch-year females weighed less and had lighter wing loading than the adult females, yet the mass and wing loading of hatch-year and adult males did not differ. Two potential benefits of lighter wing loading for hatch-year females are more favorable energetics during first-autumn migration, and slower flight speeds and greater maneuverability when hunting and flight skills are being perfected. Important questions that remain to be answered based on larger and more diverse samples include: (1) why, from the perspective of evolutionary ecology, would not hatch-year males also benefit from such advantages; (2) might this apparent sex-specific difference be a characteristic of only migratory populations; and (3) why might hatch-year males reach their adult mass sooner and when do females attain their adult mass? It is possible that hatch-year males attain hunting skills sooner or hunt prey from a size range that gives them an advantage in capture success, which could contribute to faster weight gains compared to hatch-year females.

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