WING AREAS, WING LOADINGS AND WING SPANS OF 66 SPECIES OF AFRICAN RAPTORS

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SUMMARY

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The paper provides data on the wing areas of 855 birds of 66 species and wing spans of 918 individuals of 58 species of African raptors. Two measures of wing loading were calculated for those individuals that were weighed. Wing, secondary and ulnar lengths are used to derive an index of wing area which explains 98,8 % of the variation in the mean wing areas of 46 species. A regression, derived from this relationship, can be used to estimate wing areas from the three linear measurements, all of which can be taken on museum specimens. Similarly, an index, using the sum of wing and ulnar lengths accounts for 99,5 % of the variation in the mean wing spans of 36 species. The wing dimensions of males and females, and adults and juveniles are compared in several species. For those species with adequate samples of measurements of wing area, body mass and wing span, the cost of flapping flight can be estimated with confidence.

INTRODUCTION

Wing dimensions are of biological interest for several reasons. They can be used to predict and understand the habitat selection, hunting methods, time budgets and systematic relationships of different species (e.g. Brown & Amadon 1968; Jaksić & Carothers 1985; Norberg 1986). Measurement of wings are also used to investigate the functional significance of structural, especially aerodynamic, designs (e.g. Kokshaysky 1973; Greenewalt 1975). In recent years many biologists have sought to compile energy budgets for birds, in which the energetic costs of flight are a major component. These costs are difficult to measure, but can be estimated with some confidence from wing dimensions and body mass (Masman & Klaassen 1987).

Unfortunately, many of these studies were hampered by the paucity of information on wing areas, loadings and spans. The best set of published data for raptors (Brown & Amadon 1968) provided wing areas and body masses for 56 diurnal species, but for many species only one or two individual measurements were given. In this paper, we present wing dimensions and body masses of diurnal and nocturnal African raptors and some Palaearctic species that migrate to Africa. The wing areas of 855 individuals of 66 species and wing spans of 918 birds of 58 species were measured. The body masses of these birds are also given, but Biggs *et al.* (1979) provide average masses based on larger samples for most species. The only wing areas included here that have been previously published are some of those of *Falco rupicoloides* (Kemp 1987) and *Gyps coprotheres* (Brown 1987). English names of all taxa are listed in Appendix 1.

Wing areas are difficult to measure, compared with linear dimensions such as wing lengths. Live birds or fresh specimens are required, and comparable measurements from different individuals are hard to obtain. The process of calculating areas may also be laborious. Similar difficulties hold for measurements of wing spans. As a partial solution to these problems, the measurements taken were used to provide regression equations from which both wing areas and spans can be estimated. The equations use linear measurements that can readily be obtained from dried museum skins. Wing areas and spans of raptor species represented in collections can thus be estimated.

METHODS

Our data were assembled between 1976 and 1988, mostly from birds caught in the wild. Other measurements were taken from birds kept by falconers and zoos, and dead specimens brought to museums. The following variables were recorded for most birds:

Mass (in g) — recorded using Pesola, Salter, triple-beam or other scales to accuracies of about 1 %, depending on the mass of the bird and calibration of the scale.

Wing length (in mm) — the standard measurement of the flattened wing from the wrist (carpometacarpal joint) to the tip of the longest primary feather.

Secondary length (in mm) — the length of the most distal secondary remex, flattened and measured from the wrist to the tip of the feather (see Biggs *et al.* 1978).

Ulnar length (in mm) — from the folded wrist to the inner side of the elbow joint, actually to the inner side of the distal humerus and thus an index of the length of the ulna (see Biggs *et al.* 1978).

Wing area (in cm^2) — measured from tracings of

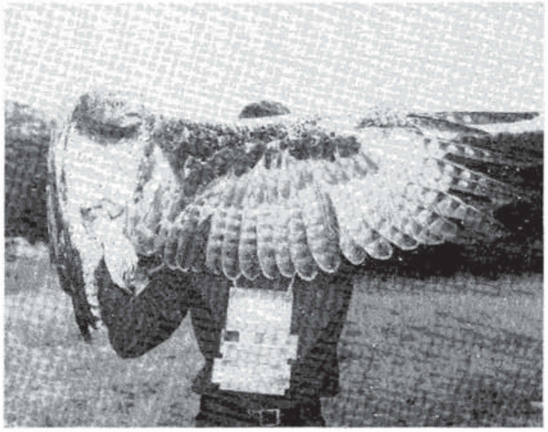

FIGURE 1

A photograph of a Martial Eagle *Polemaetus bellicosus* showing the extended wing and colour patches used to scale the projected photograph.

one wing and doubled for the area of both wings. The wing was extended so that the leading edge formed as straight a line as possible. Tracings were made either of a wing flattened onto a sheet of paper or of a photographic slide of an open wing (Fig. 1). The slide was projected onto a piece of paper so that the image was the same size as the actual wing, using a scale to match the sizes. Because wings held vertically were slightly more concave than those flattened onto paper, a correction factor was applied to the area calculated from photographed wings (see Appendix 2 for details of the method). Our wing areas do not include the area of the body or tail (cf. Norberg 1986).

Wing span (in mm) — on birds in the hand, the wings were extended to form a straight line and wing spans measured as either (1) the distance between the wing tips, (2) double the distance from one tip to the centre (the vertebral spines) of the dorsal surface between the wings, or (3) double the distance from the tip of a wing to the proximal edge of its humerus + the distance from the proximal edge of one humerus to the same position on the other. On projected slides, wing span was double the distance from the tip of a wing to its base (where it joins the body anteriorally) + the distance between the bases of the two wings.

Because the shape of the extended wing is roughly rectangular (Fig. 1), we multiplied the sum of the wing and ulnar lengths with secondary length to obtain a wing area index for each bird. The area index/100 is in cm^2, because the lengths from which it is derived are measured in mm. Two indices of wing loading were calculated for each bird: (a) mass loading is body mass divided by wing area, i.e. g/cm^2, (b) while linear loading is the cube root of mass divided by the square root of wing area, $g^{0,33}/cm$ (see Jaksić & Carothers 1985). Aspect ratios (wing span^2/wing area) for each species can be calculated from the data in the paper. We present means, standard deviations and sample sizes for each species for which the wing areas or spans of three or more individuals were measured, and full details for each bird when only one or two individuals were measured. Copies of the original data for each individual bird have been deposited at the Percy Fitzpatrick Institute of African Ornithology (Cape Town) and ornithological sections at the Durban Natural History Museum, National Museum (Bloemfontein), Transvaal Museum (Pretoria) and State Museum (Windhoek).

RESULTS AND DISCUSSION

Tables 1 and 2 present data on wing areas, body mass, wing length, secondary length, ulnar length and wing area indices. Some of the largest eagles and vultures, *Polemaetus bellicosus* (3 932 g), *Aquila verreauxii* (3 316 g), *Gypaetus barbatus* (5 397 g) and *Gyps coprotheres* (9 289 g), were more than 100× heavier than the smallest raptors, *Polihierax semitorquatus* (59 g), *Glaucidium perlatum* (88 g), *G. capense* (93 g) and *Otus senegalensis* (80 g). However, the ratio between the largest and smallest wing areas was about 40, from about 200 cm^2 in the smallest species to 8 000–9 000 cm^2 in the largest vulture (Table 1). These disparities in scaling have different effects on measures of wing loading. Mass loading, reflecting the actual mass supported by the wings in flight, varies from about 0,21 in *Falco naumanni* and *F. vespertinus* to *Gyps coprotheres* which carries the heaviest load of 1,09 g/cm^2. Linear loading, which corrects for the effects of mass and area having different scaling factors, varies to a lesser degree, from 0,172 (*Polyboroides typus*) to 0,284 (*G. perlatum*) (Table 1). These two species therefore have the largest and smallest wings in relation to body mass, respectively.

We expected that measurements of wing areas would be highly variable because (a) there was a fair degree of subjectivity in judging precisely where the wing ended proximally (see Fig. 1), (b) we neither consistently excluded nor included wing slots and gaps produced by moulting feathers, and (c) tracings of wings were obtained from two rather different sources (photographs and live birds). While the wing areas in Table 1 are, indeed, quite variable, the variation is similar to that for wing area indices which were calculated from linear measurements that can be taken easily and repeatably.

Tables 3 & 4 provide data on wing spans. The variety of methods (see METHODS) used to measure wing span yielded similar results. For example, wing spans measured off photographs of *Melierax canorus* averaged 1 107,3 cm (S.D. = 48,1; n = 27), compared with a mean of 1 108,5 cm (S.D. = 67,9; n = 204) obtained from birds in the hand by doubling the distance from the tip of a wing to the proximal edge of its humerus + the distance between the proximal edges of the two

TABLE 1
WING AREAS, BODY MASSES, WING LOADINGS AND OTHER DIMENSIONS [MEAN ± STANDARD DEVIATION (N)] OF 48 SPECIES OF AFRICAN RAPTORS FOR WHICH THREE OR MORE INDIVIDUALS WERE AVAILABLE

	Wing Area	Body Mass	Linear Loading	Mass Loading	Wing Length	Secondary Length	Ulnar Length	Wing Area Index
Falco biarmicus	1 123,1 ± 182,1 (35)	546,6 ± 72,3 (34)	0,246 ± 0,016(34)	0,496 ± 0,066 (34)	321,4 ± 22,1 (27)	164,1 ± 12,2 (27)	99,0 ± 4,8 (27)	692,6 ± 90,3 (27)
Falco chicquera	591,6 ± 41,9 (9)	216,2 ± 23,2 (9)	0,247 ± 0,014 (9)	0,368 ± 0,052 (9)	233,7 ± 6,6 (9)	124,6 ± 2,9 (8)	68,4 ± 1,9 (9)	379,8 ± 11,7 (8)
Falco dickinsoni	523,0 ± 47,3 (11)	189,0 ± 16,8 (11)	0,251 ± 0,010 (11)	0,363 ± 0,031 (11)	221,6 ± 8,6 (11)	105,3 ± 2,8 (11)	64,7 ± 3,5 (11)	301,6 ± 18,1 (11)
Falco naumanni	557,6 ± 36,8 (10)	121,0 ± 17,1 (10)	0,209 ± 0,012 (10)	0,218 ± 0,034 (10)	233,8 ± 5,3 (10)	110,5 ± 3,5 (10)	65,6 ± 5,8 (10)	330,9 ± 14,2 (10)
Falco rupicoloides	844,9 ± 81,8 (61)	255,3 ± 20,6 (59)	0,219 ± 0,011 (59)	0,306 ± 0,034 (59)	281,4 ± 9,7 (54)	138,9 ± 6,2 (54)	81,0 ± 3,2 (52)	504,3 ± 35,8 (52)
Falco tinnunculus	634,4 ± 51,4 (42)	181,5 ± 18,1 (37)	0,224 ± 0,009 (37)	0,286 ± 0,030 (37)	244,5 ± 6,8 (35)	121,5 ± 4,9 (34)	69,6 ± 2,6 (35)	382,1 ± 20,5 (32)
Falco vespertinus	543,7 ± 29,3 (5)	112,5 ± 10,3 (4)	0,208 ± 0,005 (4)	0,208 ± 0,013 (4)	233,0 ± 7,1 (5)	108,8 ± 1,7 (5)	64,8 ± 1,9 (5)	323,9 ± 5,2 (5)
Polihierax semitorquatus	204,5 ± 24,6 (13)	59,5 ± 4,6 (13)	0,274 ± 0,017 (13)	0,294 ± 0,037 (13)	119,4 ± 2,2 (12)	76,3 ± 3,1 (12)	40,9 ± 1,2 (12)	122,3 ± 6,0 (12)
Tyto alba	1 142,9 ± 85,2 (18)	348,9 ± 38,9 (16)	0,209 ± 0,011 (16)	0,309 ± 0,039 (16)	283,6 ± 8,9 (18)	167,3 ± 5,9 (18)	104,3 ± 4,2 (18)	649,1 ± 31,5 (18)
Tyto capensis	1 520,1 ± 108,0 (10)	413,9 ± 46,0 (9)	0,191 ± 0,011 (9)	0,274 ± 0,040 (9)	329,6 ± 11,6 (9)	187,3 ± 4,0 (8)	127,0 ± 3,4 (9)	851,1 ± 31,2 (8)
Asio capensis	1 243,0 ± 105,5 (5)	353,3 ± 36,6 (3)	0,197 ± 0,002 (3)	0,274 ± 0,012 (3)	280,2 ± 5,8 (5)	176,0 ± 5,4 (5)	109,8 ± 3,5 (5)	686,5 ± 26,0 (5)
Bubo africanus	2 057,3 ± 175,0 (37)	741,6 ± 93,9 (31)	0,199 ± 0,007 (31)	0,358 ± 0,035 (31)	338,9 ± 13,3 (37)	227,2 ± 8,6 (36)	136,5 ± 4,8 (37)	1 082,4 ± 64,7 (36)
Bubo capensis	2 357,9 ± 169,5 (6)	1 064,2 ± 157,0 (6)	0,210 ± 0,007 (6)	0,450 ± 0,046 (6)	363,0 ± 23,4 (5)	244,6 ± 16,6 (5)	152,4 ± 6,7 (5)	1 264,9 ± 153,4 (5)
Glaucidium capense	294,8 ± 41,6 (4)	93,3 ± 7,1 (4)	0,266 ± 0,015 (4)	0,320 ± 0,035 (4)	132,8 ± 4,2 (4)	104,5 ± 3,8 (4)	54,9 ± 2,0 (4)	196,2 ± 10,3 (4)
Glaucidium perlatum	247,8 ± 21,3 (17)	88,4 ± 14,0 (16)	0,284 ± 0,017 (16)	0,360 ± 0,058 (16)	106,9 ± 4,1 (17)	84,9 ± 2,6 (17)	46,2 ± 2,3 (17)	134,3 ± 6,5 (17)
Otus leucotis	676,9 ± 97,5 (3)	225,7 ± 28,9 (3)	0,235 ± 0,018 (3)	0,339 ± 0,061 (3)	196,3 ± 2,5 (3)	137,0 ± 5,1 (3)	79,0 ± 1,4 (3)	377,3 ± 17,0 (3)
Otus senegalensis	336,8 ± 10,0 (3)	80,1 ± 13,7 (3)	0,234 ± 0,015 (3)	0,239 ± 0,043 (3)	138,3 ± 2,1 (3)	97,5 ± 0,5 (2)	49,0 ± 0,0 (2)	182,8 ± 3,4 (2)
Strix woodfordii	1 203,1 ± 44,6 (7)	344,8 ± 22,3 (6)	0,202 ± 0,003 (6)	0,286 ± 0,014 (6)	249,7 ± 9,6 (6)	179,3 ± 9,3 (6)	89,5 ± 3,8 (6)	608,8 ± 46,6 (6)
Aquila nipalensis	4 167,9 ± 257,6 (4)	3 025,0 ± 486,7 (4)	0,224 ± 0,012 (4)	0,726 ± 0,115 (4)	561,0 ± 28,8 (4)	355,3 ± 12,9 (4)	229,3 ± 6,8 (4)	2 812,0 ± 228,6 (4)
Aquila rapax	3 956,1 ± 324,5 (10)	2 499,0 ± 391,2 (10)	0,216 ± 0,013 (10)	0,634 ± 0,102 (10)	523,7 ± 25,8 (7)	323,9 ± 15,9 (7)	212,3 ± 13,2 (7)	2 388,5 ± 225,5 (7)
Aquila verreauxii	5 138,6 ± 497,1 (9)	3 315,7 ± 806,5 (7)	0,204 ± 0,010 (7)	0,619 ± 0,108 (7)	602,3 ± 21,8 (8)	399,4 ± 14,9 (8)	239,9 ± 8,0 (8)	3 366,2 ± 223,2 (8)
Aquila wahlbergi	2 655,7 ± 193,4 (9)	1 209,4 ± 172,5 (9)	0,206 ± 0,007 (9)	0,454 ± 0,046 (9)	430,7 ± 10,9 (9)	259,4 ± 6,0 (9)	161,4 ± 8,8 (9)	1 536,7 ± 68,5 (9)
Hieraaetus ayresii	2 277,9 ± 271,3 (4)	988,3 ± 274,0 (4)	0,207 ± 0,011 (4)	0,428 ± 0,077 (4)	386,0 ± 11,6 (4)	245,0 ± 6,1 (4)	145,5 ± 3,0 (4)	1 302,4 ± 49,1 (4)
Hieraaetus spilogaster	2 751,8 ± 248,2 (21)	1 479,9 ± 129,0 (21)	0,218 ± 0,009 (21)	0,540 ± 0,052 (21)	433,1 ± 15,2 (21)	283,6 ± 11,7 (21)	168,3 ± 7,2 (21)	1 707,2 ± 120,4 (21)
Polemaetus bellicosus	6 398,1 ± 830,9 (21)	3 931,8 ± 645,5 (20)	0,196 ± 0,009 (20)	0,609 ± 0,070 (20)	623,2 ± 31,7 (10)	408,8 ± 25,0 (10)	265,6 ± 16,9 (10)	3 643,9 ± 398,7 (10)
Buteo augur	2 417,5 ± 257,9 (6)	973,2 ± 118,5 (5)	0,203 ± 0,004 (5)	0,406 ± 0,007 (5)	414,2 ± 10,3 (5)	276,8 ± 12,6 (5)	150,2 ± 1,6 (5)	1 563,5 ± 98,9 (5)
Buteo buteo	1 872,5 ± 197,5 (17)	731,0 ± 87,2 (17)	0,209 ± 0,012 (17)	0,393 ± 0,053 (17)	368,2 ± 9,9 (17)	221,5 ± 9,6 (17)	127,3 ± 5,2 (17)	1 098,3 ± 67,4 (17)
Buteo rufofuscus	2 759,6 ± 325,4 (19)	1 059,4 ± 184,0 (18)	0,193 ± 0,010 (18)	0,381 ± 0,052 (18)	411,8 ± 15,7 (12)	274,3 ± 15,9 (12)	146,6 ± 8,1 (12)	1 534,3 ± 140,5 (12)
Buteo trizonatus	1 627,8 ± 175,3 (3)	602,7 ± 99,6 (3)	0,209 ± 0,010 (3)	0,370 ± 0,049 (3)	344,3 ± 12,0 (3)	219,7 ± 11,8 (3)	113,3 ± 2,1 (3)	1 006,5 ± 77,4 (3)
Circaetus cinereus	4 054,4 ± 130,2 (3)	2 050,0 ± 70,7 (3)	0,200 ± 0,001 (3)	0,506 ± 0,004 (3)	532,3 ± 2,1 (3)	310,0 ± 8,2 (3)	204,3 ± 3,7 (3)	2 283,8 ± 64,1 (3)
Circaetus pectoralis	3 686,4 ± 382,3 (22)	1 457,7 ± 142,8 (21)	0,187 ± 0,010 (21)	0,397 ± 0,049 (21)	525,1 ± 9,7 (20)	310,9 ± 6,5 (20)	211,8 ± 7,7 (20)	2 290,5 ± 67,1 (20)
Terathopius ecaudatus	3 530,3 ± 286,4 (3)	2 391,7 ± 218,3 (3)	0,226 ± 0,016 (3)	0,688 ± 0,125 (3)	490,0 ± 5,0 (2)	288,0 ± 2,0 (2)	223,5 ± 1,5 (2)	2 055,0 ± 33,0 (2)
Haliaeetus vocifer	5 456,8 ± 843,5 (3)	2 683,3 ± 417,0 (3)	0,189 ± 0,007 (3)	0,492 ± 0,030 (3)	550,0 ± 12,3 (3)	375,0 ± 24,8 (3)	230,0 ± 8,2 (3)	2 929,4 ± 257,4 (3)
Circus ranivorus	1 690,1 ± 205,7 (3)	470,0 ± 41,4 (3)	0,190 ± 0,010 (3)	0,281 ± 0,031 (3)	371,3 ± 8,4 (3)	211,7 ± 4,8 (3)	127,3 ± 4,2 (3)	1 056,0 ± 46,9 (3)
Elanus caeruleus	890,6 ± 57,4 (170)	243,5 ± 22,2 (168)	0,209 ± 0,008 (168)	0,274 ± 0,025 (168)	266,8 ± 7,8 (158)	145,6 ± 5,3 (164)	88,7 ± 3,3 (169)	518,3 ± 28,0 (156)
Milvus migrans	2 152,0 ± 171,5 (17)	630,7 ± 88,7 (13)	0,185 ± 0,010 (13)	0,294 ± 0,041 (13)	424,9 ± 21,4 (17)	225,1 ± 9,0 (17)	147,6 ± 6,2 (17)	1 290,6 ± 102,9 (17)
Milvus parasitus	2 139,6 ± 252,6 (18)	656,0 ± 81,4 (10)	0,183 ± 0,009 (10)	0,291 ± 0,032 (10)	413,8 ± 14,0 (18)	219,6 ± 12,6 (17)	138,7 ± 5,3 (18)	1 212,6 ± 91,5 (17)
Polyboroides typus	2 898,4 ± 168,2 (5)	785,0 ± 100,1 (4)	0,172 ± 0,008 (4)	0,275 ± 0,035 (4)	453,0 ± 15,0 (5)	308,8 ± 18,3 (5)	138,4 ± 8,3 (5)	1 825,4 ± 108,5 (5)
Accipiter badius	512,6 ± 70,9 (9)	127,4 ± 8,6 (9)	0,223 ± 0,012 (9)	0,252 ± 0,026 (9)	191,2 ± 7,6 (9)	121,4 ± 5,7 (9)	62,0 ± 3,3 (9)	303,3 ± 23,6 (9)
Accipiter melanoleucos	1 542,6 ± 240,6 (5)	746,0 ± 110,9 (5)	0,232 ± 0,008 (5)	0,485 ± 0,019 (5)	308,0 ± 26,9 (5)	210,0 ± 14,5 (5)	110,2 ± 5,4 (5)	882,6 ± 126,3 (5)
Accipiter tachiro	1 016,8 ± 222,1 (12)	326,5 ± 90,1 (11)	0,215 ± 0,012 (11)	0,317 ± 0,044 (11)	226,9 ± 18,2 (7)	173,4 ± 20,9 (7)	76,7 ± 6,1 (7)	530,7 ± 102,1 (7)
Kaupifalco monogrammicus	748,8 ± 45,2 (8)	303,1 ± 29,2 (7)	0,246 ± 0,003 (7)	0,408 ± 0,019 (7)	226,0 ± 9,3 (6)	138,8 ± 4,6 (6)	79,0 ± 3,7 (7)	423,9 ± 25,6 (6)
Melierax canorus	1 723,6 ± 211,6 (80)	724,2 ± 99,5 (76)	0,217 ± 0,009 (76)	0,421 ± 0,040 (76)	354,2 ± 16,1 (65)	216,1 ± 10,8 (64)	124,5 ± 5,5 (65)	1 036,7 ± 94,5 (64)
Melierax metabates	1 487,7 ± 121,4 (13)	635,4 ± 77,8 (12)	0,223 ± 0,010 (12)	0,427 ± 0,049 (12)	314,7 ± 9,6 (13)	203,9 ± 14,2 (13)	113,8 ± 5,4 (13)	861,4 ± 57,4 (13)
Micronisus gabar	544,1 ± 65,5 (4)	175,0 ± 2,9 (3)	0,232 ± 0,004 (3)	0,302 ± 0,010 (3)	199,3 ± 6,6 (3)	131,7 ± 7,4 (3)	63,7 ± 2,6 (3)	346,9 ± 30,2 (3)
Gypaetus barbatus	7 370,9 ± 410,8 (18)	5 396,9 ± 566,6 (16)	0,204 ± 0,010 (16)	0,731 ± 0,091 (16)	767,8 ± 19,4 (16)			
Gyps coprotheres	8 541,3 ± 508,4 (9)	9 288,9 ± 823,9 (9)	0,227 ± 0,009 (9)	1,090 ± 0,104 (9)	716,1 ± 24,7 (9)			
Sagittarius serpentarius	5 577,5 ± 370,2 (8)	3 677,1 ± 326,4 (7)	0,207 ± 0,011 (7)	0,664 ± 0,083 (7)	638,9 ± 22,9 (8)	381,9 ± 11,1 (8)	214,0 ± 6,2 (8)	3 258,3 ± 159,1 (8)

TABLE 2
WING AREAS, BODY MASSES, WING LOADINGS AND OTHER DIMENSIONS OF 18 SPECIES OF AFRICAN RAPTORS FOR WHICH ONLY ONE OR TWO INDIVIDUALS WERE AVAILABLE

Species	Wing Area	Body Mass	Linear Loading	Mass Loading	Wing Length	Secondary Length	Ulnar Length	Wing Area Index
Falco concolor	575,3	125	0,208	0,217	266	120	73	407
Falco amurensis	567,5	125	0,210	0,220	214	106	54	284
Falco amurensis	584,0	133	0,211	0,228	244	115	66	357
Falco peregrinus	1 033,3	477	0,243	0,462	283	124	86	458
Falco peregrinus	1 002,6				317	152	98	631
Bubo lacteus	4 225,1	1 980	0,193	0,469	435	295	195	1 859
Accipiter minullus	272,6	68	0,247	0,249	143	104	49	200
Accipiter minullus	427,5				152	110	55	228
Accipiter ovampensis	654,9	175	0,219	0,267	225	142	71	420
Accipiter rufiventris	748,4	180	0,206	0,241	235	143	77	446
Aviceda cuculoides	1 295,3	220	0,168	0,170	305	189	98	762
Circus pygargus	1 555,6	325	0,174	0,209	350	190	112	878
Aquila pomarina	3 091,9	1 408	0,202	0,455	475	280	186	1 851
Circaetus cinerascens	2 678,2	1 126	0,201	0,420	390	275	160	1 512
Circaetus fasciolatus	2 332,0	1 110	0,214	0,476	360	256	137	1 272
Circaetus fasciolatus	2 340,2	950	0,203	0,406	362	255	132	1 260
Macheiramphus alcinus	1 504,3	600	0,217	0,399	364	189	127	928
Macheiramphus alcinus	1 427,6	620	0,226	0,434	355	185	126	890
Hieraaetus pennatus	1 612,0	582	0,208	0,361	345	209	129	991
Heraaetus pennatus	2 024,2	810	0,207	0,400				
Lophaetus occipitalis	2 705,3	980	0,191	0,362	405	270	142	1 477
Stephanoaetus coronatus	6 390,6	4 200	0,202	0,657				
Stephanoaetus coronatus	4 440,0	2 550	0,205	0,574	470	372	174	2 396
Trigonoceps occipitalis	6 011,0	3 970	0,204	0,660	640	385	316	3 681
Trigonoceps occipitalis	6 528,2				622	379	297	3 483
Gyps africanus	7 529,0	5 800	0,207	0,770	570	390	310	3 432

humeri. *Glaucidium* owls and *Polihierax semitorquatus* have the smallest wing spans (372–404 mm), in contrast to those of *Gyps coprotheres* (2 573 mm) and *Gypaetus barbatus* (2 577 mm).

Data were available to examine sexual differences in wing dimensions of four species (Table 5). The wing areas, body masses and linear dimensions of females were significantly greater than those of males in all species, except for the wing lengths of *Elanus caeruleus*. Females carried greater loads (mass loading) than males in *E. caeruleus* and *Melierax canorus*. Male *Falco biarmicus* had relatively heavier loads than females, the only species to show any sexual difference in linear loading.

Age differences in wing dimensions could be examined in three species (Table 6). Adult *Elanus caeruleus* were heavier and had longer wings than juveniles which carried lower linear and mass loadings. There were no significant differences between adult and juvenile *Melierax canorus*. Adult *Gypaetus barbatus* were heavier, had longer wings and carried greater loads (both mass and linear loading) than juveniles. Their wing spans were, however, greater and their wings were narrower and smaller in area than those of juveniles (Table 6, and Brown 1988). The importance of these sexual and age differences in wing dimensions is not clear.

The correlation between mean wing area for 46 species in Table 1 and mean wing area indices was highly significant and showed that the index accounted for 98,8 % of the variation in wing area (Fig. 2, Table 7). The wing area (A) of raptor species can thus be confidently estimated from the wing area index (I) using the following regression

$$A = 1{,}665(I) + 35{,}820$$

There was also a strong correlation between the mean wing spans of different species and the sum of wing and ulnar lengths as an index of span; this index accounted for 99,5 % of the variation between species. The regression to estimate wing span (S) from the sum of wing and ulnar lengths (L) is

$$S = 2{,}403(L) - 15{,}042$$

Significant correlations between wing areas and wing area indices were also found for individuals of some species (Table 7) but the scatter of data was greater (e.g. Fig. 3). We suspect that much of the scatter was due to errors of measurement, so with sufficient care it should be possible to estimate wing areas for individual birds.

Masman & Klaassen (1987) provide a multiple regression to estimate the energetic cost of flapping flight. The equation uses body mass (M), wing span (S) and wing area (A) that together account for 84 % of the variation in flight costs (FC

TABLE 3
WING SPANS OF 40 SPECIES OF AFRICAN RAPTORS FOR WHICH THREE OR MORE INDIVIDUALS WERE AVAILABLE

Species	Mean	Std. Dev.	No.
Falco biarmicus	1 029,1	73,0	32
Falco chicquera	686,6	32,1	10
Falco dickinsoni	669,1	32,5	11
Falco naumanni	721,7	27,8	3
Falco rupicoloides	836,0	39,2	72
Falco tinnunculus	713,9	35,0	130
Polihierax semitorquatus	371,7	18,6	9
Tyto alba	908,6	25,0	11
Bubo africanus	1 132,9	70,5	26
Bubo capensis	1 249,3	70,2	5
Bubo lacteus	1 634,7	77,0	3
Glaucidium capense	403,6	22,9	4
Glaucidium perlatum	386,2	16,7	32
Otus leucotis	666,8	34,1	4
Otus senegalensis	467,8	20,9	12
Strix woodfordii	787,9	19,9	6
Aquila rapax	1 823,2	121,0	15
Aquila verreauxii	1 994,2	79,0	5
Aquila wahlbergi	1 407,3	78,2	11
Hieraaetus pennatus	1 223,2	100,8	4
Hieraaetus spilogaster	1 416,7	85,2	36
Polemaetus bellicosus	2 119,0	188,2	10
Buteo augur	1 315,5	64,6	22
Buteo buteo	1 188,4	46,9	11
Buteo rufofuscus	1 319,0	56,7	9
Circaetus cinereus	1 640,7	71,7	3
Circaetus pectoralis	1 776,1	59,8	23
Elanus caeruleus	844,4	26,8	27
Milvus migrans	1 309,0	41,4	9
Milvus parasitus	1 294,7	43,6	7
Accipiter badius	578,4	38,8	34
Accipiter melanoleucos	1 017,0	55,1	3
Accipiter tachiro	698,4	44,8	3
Kaupifalco monogrammicus	785,0	43,8	9
Melierax metabates	1 011,9	40,4	17
Melierax canorus	1 108,3	66,0	229
Micronisus gabar	598,1	60,6	7
Gypaetus barbatus	2 576,8	57,1	17
Gyps coprotheres	2 573,3	93,0	6
Sagittarius serpentarius	2 120,4	106,8	8

in Watts) between species.

$$FC = 17{,}360 M^{1,013} S^{-4,236} A^{1,926}$$

The costs of non-soaring flight can therefore be estimated for those species in Tables 1 and 3 with substantial samples of data for these three variables. Reasonable estimates of flight costs should also be obtainable for other raptor species. Museum specimens can provide wing, ulnar and secondary lengths from which wing areas and spans can be predicted. In the absence of measured weights, reliable estimates of these can be obtained from regression equations that express the close relationship between egg size and body weight (Hoyt 1979; Kemp in press). While such estimates will be subject to some error, they should provide better information than that currently available for species that cannot be studied directly.

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TABLE 4
WING SPANS OF 18 SPECIES OF AFRICAN RAPTORS FOR WHICH ONLY ONE OR TWO INDIVIDUALS WERE AVAILABLE

Species	Wing Span
Falco concolor	709,8
Falco peregrinus	1 032,0
Falco vespertinus	681,2
Falco vespertinus	713,2
Tyto capensis	996,5
Tyto capensis	1 080,0
Asio capensis	860,8
Asio capensis	970,0
Aquila nipalensis	2 279,3
Aquila nipalensis	1 920,7
Aquila pomarina	1 501,0
Hieraaetus ayresii	1 233,3
Hieraaetus ayresii	1 239,8
Stephanoaetus coronatus	1 520,0
Circaetus cinerascens	1 135,0
Terathopius ecaudatus	1 861,9
Haliaeetus vocifer	1 900,0
Circus pygargus	1 100,0
Accipiter minullus	385,4
Accipiter ovampensis	667,4
Accipiter rufiventris	720,3
Aviceda cuculoides	906,5
Trigonoceps occiptalis	2 162,5

APPENDIX 1

ENGLISH NAMES OF ALL SPECIES LISTED IN THIS PAPER.

Falco amurensis	Eastern Redfooted Kestrel
Falco biarmicus	Lanner Falcon
Falco chicquera	Rednecked Falcon
Falco concolor	Sooty Falcon
Falco dickinsoni	Dickinson's Kestrel
Falco naumanni	Lesser Kestrel
Falco peregrinus	Peregrine Falcon
Falco rupicoloides	Greater Kestrel
Falco tinnunculus	Rock Kestrel
Falco vespertinus	Western Redfooted Kestrel
Polihierax semitorquatus	Pygmy Falcon
Tyto alba	Barn Owl
Tyto capensis	Grass Owl
Asio capensis	Marsh Owl
Bubo africanus	Spotted Eagle Owl
Bubo capensis	Cape Eagle Owl
Bubo lacteus	Giant Eagle Owl
Glaucidium capense	Barred Owl
Glaucidium perlatum	Pearlspotted Owl
Otus leucotis	Whitefaced Owl
Otus senegalensis	African Scops Owl
Strix woodfordii	Wood Owl
Aquila nipalensis	Steppe Eagle
Aquila pomarina	Lesser Spotted Eagle
Aquila rapax	Tawny Eagle
Aquila verreauxii	Black Eagle
Aquila wahlbergi	Wahlberg's Eagle
Hieraaetus ayresii	Ayres' Eagle
Hieraaetus pennatus	Booted Eagle
Hieraaetus spilogaster	African Hawk Eagle
Lophaetus occipitalis	Longrested Eagle
Polemaetus bellicosus	Martial Eagle
Stephanoaetus coronatus	Crowned Eagle
Buteo augur	Augur Buzzard
Buteo buteo	Steppe Buzzard
Buteo rufofuscus	Jackal Buzzard
Buteo trizonatus	Forest Buzzard
Circaetus cinereus	Brown Snake Eagle
Circaetus fasciolatus	Southern Banded Snake Eagle
Circaetus cinerascens	Western Banded Snake Eagle
Circaetus pectoralis	Blackbreasted Snake Eagle

TABLE 5

WING AREAS AND OTHER DIMENSIONS OF MALE AND FEMALE *ELANUS CAERULEUS*, *FALCO RUPICOLOIDES*, *F. BIARMICUS* AND *MELIERAX CANORUS*. * $p < 0,05$; ** $p < 0,025$; *** $p < 0,01$; **** $p < 0,005$ — t-tests

Species		Wing Area	Body Mass	Linear Loading	Mass Loading	Wing Length	Secondary Length	Ulnar Length	Wing Area Index
E. CAERULEUS									
Males	Mean	880,83	234,83	0,208	0,267	265,47	144,44	87,40	510,61
	S.D.	48,20	17,71	0,007	0,023	8,40	4,90	2,64	27,14
	N	65	65	65	65	53	52	55	51
	diff	****	****	N.S.	**	N.S.	****	***	****
Females	Mean	930,79	257,60	0,209	0,277	266,08	148,32	88,75	526,47
	S.D.	46,98	19,76	0,007	0,023	8,02	5,91	2,49	29,33
	N	47	47	47	47	38	38	40	38
F. BIARMICUS									
Males	Mean	1 050,40	520,27	0,251	0,508	305,67	154,20	95,67	618,94
	S.D.	172,69	71,46	0,016	0,072	9,91	3,31	2,55	23,02
	N	23	22	22	22	15	15	15	15
	diff	****	****	***	N.S.	****	****	****	****
Females	Mean	1 262,40	594,92	0,237	0,474	341,08	176,50	103,25	784,68
	S.D.	100,24	43,04	0,010	0,047	16,85	6,84	3,54	49,26
	N	12	12	12	12	12	12	12	12
F. RUPICOLOIDES									
Males	Mean	809,57	247,75	0,221	0,307	278,06	135,56	79,88	485,53
	S.D.	60,52	15,85	0,008	0,024	9,00	4,32	2,29	27,05
	N	16	16	16	16	16	16	16	16
	diff	*	***	N.S.	N.S.	****	****	****	****
Females	Mean	855,85	263,05	0,220	0,311	287,74	143,63	83,11	533,00
	S.D.	93,28	16,05	0,013	0,039	9,28	6,33	2,38	33,07
	N	19	19	19	19	19	19	19	19
M. CANORUS									
Males	Mean	1 560,84	647,14	0,219	0,418	342,00	206,86	120,37	956,56
	S.D.	129,27	41,82	0,010	0,045	8,33	4,16	3,16	31,30
	N	35	35	35	35	35	35	35	35
	diff	****	****	N.S.	**	****	****	****	****
Females	Mean	1 849,69	808,70	0,217	0,439	396,96	227,07	129,61	1 134,68
	S.D.	145,79	50,88	0,007	0,030	8,43	4,73	3,29	41,34
	N	28	27	27	27	28	28	28	28

The sexes of *Elanus caeruleus* were determined from the behaviour of individually marked birds and from a discriminant analysis of various body measurements (Mendelsohn 1981). Individually marked male and female *Falco rupicoloides* were distinguished by their behaviour and social interactions (Kemp 1987). The wing and secondary lengths of *Falco biarmicus* formed two distinct clusters, so those with wings of <330 mm and secondary lengths of <162 mm were assumed to be males. Likewise, male *Melierax canorus* were considered to have wing lengths <350 mm and secondary lengths <215 mm; females were those with wing lengths >360 mm and secondary lengths >220 mm.

TABLE 6

WING AREAS AND OTHER DIMENSIONS OF ADULT AND JUVENILE OR SUBADULT *ELANUS CAERULEUS*, *MELIERAX CANORUS* AND *GYPAETUS BARBATUS*. ADULT *G. BARBATUS* EXCEEDED FIVE YEARS OF AGE, JUVENILES WERE LESS THAN TWO YEARS OLD (BROWN 1988). * $p < 0,05$; ** $p < 0,025$; *** $p < 0,01$; **** $p < 0,005$ — t-tests

Species		Wing Area	Body Mass	Linear Loading	Mass Loading	Wing Length	Secondary Length	Ulnar Length	Wing Area Index
E. CAERULEUS									
Adults	Mean	897,78	246,49	0,209	0,275	267,40	145,93	88,29	519,65
	S.D.	55,46	21,68	0,008	0,026	7,62	5,28	2,83	26,92
	N	130	130	130	130	120	127	129	120
	diff	N.S.	****	**	****	***	N.S.	N.S.	N.S.
Juveniles	Mean	885,98	230,43	0,206	0,260	263,09	144,67	88,83	510,66
	S.D.	46,47	19,50	0,006	0,019	7,72	5,73	3,84	31,65
	N	24	23	23	23	22	21	24	20
M. CANORUS									
Adults	Mean	1 735,26	726,05	0,216	0,421	355,38	216,08	124,31	1 039,32
	S.D.	208,47	97,77	0,008	0,037	16,15	10,93	5,50	95,88
	N	62	59	59	59	52	51	52	51
	diff	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Juveniles	Mean	1 683,50	717,76	0,217	0,423	349,23	216,00	125,08	1 026,31
	S.D.	217,12	114,12	0,011	0,051	14,84	10,29	5,55	88,34
	N	18	17	17	17	13	13	13	13
G. BARBATUS									
Adults	Mean	7 122,76	5 710,00	0,212	0,802	786,00			
	S.D.	366,72	383,93	0,005	0,047	13,56			
	N	5	5	5	5	5			
	diff	**	**	****	****	****			
Juveniles	Mean	7 670,87	5 016,67	0,195	0,656	758,33			
	S.D.	298,80	561,74	0,009	0,083	12,13			
	N	6	6	6	6	6			

TABLE 7

CORRELATION COEFFICIENTS AND REGRESSION SLOPES AND INTERCEPTS FOR RELATIONSHIPS BETWEEN WING AREAS AND WING AREA INDICES FOR DIFFERENT SPECIES AND INDIVIDUALS OF VARIOUS SPECIES. THE LAST LINE PROVIDES THESE DATA FOR WING SPANS IN RELATION TO WING + ULNAR LENGTHS FOR DIFFERENT SPECIES

	r	r^2	Intercept	Intercept (S.E.)	n	Slope	Slope (S.E.)
Wing Area (all spp.)	0,994	0,988	35,820	175,760	46	1,665	0,028
Falco biarmicus	0,775	0,600	44,830	117,160	27	1,537	0,250
Falco tinnunculus	0,537	0,288	133,910	42,880	32	1,291	0,370
Bubo africanus	0,392	0,153	903,600	166,030	36	1,062	0,425
Melierax canorus	0,758	0,575	88,100	127,500	64	1,544	0,169
Hieraeetus spilogaster	0,558	0,311	789,890	216,600	21	1,149	0,393
Elanus caeruleus	0,543	0,295	304,459	49,345	156	1,132	0,141
Milvus migrans	0,581	0,338	900,890	148,500	17	0,969	0,350
Milvus parasitus	0,704	0,496	− 9,370	171,620	17	1,748	0,455
Wing Span (all spp.)	0,997	0,995	−15,042	36,184	36	2,403	0,030

APPENDIX 1 CONTINUED

Terathopius ecaudatus	Bateleur
Haliaeetus vocifer	Fish Eagle
Aviceda cuculoides	Cuckoo Hawk
Circus pygargus	Montagu's Harrier
Circus ranivorus	African Marsh Harrier
Macheiramphus alcinus	Bat Hawk
Elanus caeruleus	Blackshouldered Kite
Milvus migrans	Black Kite
Milvus parasitus	Yellowbilled Kite
Polyboroides typus	Gymnogene
Accipiter badius	Littlebanded Goshawk
Accipiter melanoleucos	Black Sparrowhawk
Accipiter minullus	Little Sparrowhawk
Accipiter ovampensis	Ovambo Sparrowhawk
Accipiter rufiventris	Redbreasted Sparrowhawk
Accipiter tachiro	African Goshawk
Kaupifalco mongrammicus	Lizard Buzzard
Melierax canorus	Pale Chanting Goshawk
Melierax metabates	Dark Chanting Goshawk
Micronisus gabar	Gabar Goshawk
Gypaetus barbatus	Bearded Vulture
Gyps africanus	Whitebacked Vulture
Gyps coprotheres	Cape Vulture
Trignoceps occipitalis	Whiteheaded Vulture
Sagittarius serpentarius	Secretary Bird

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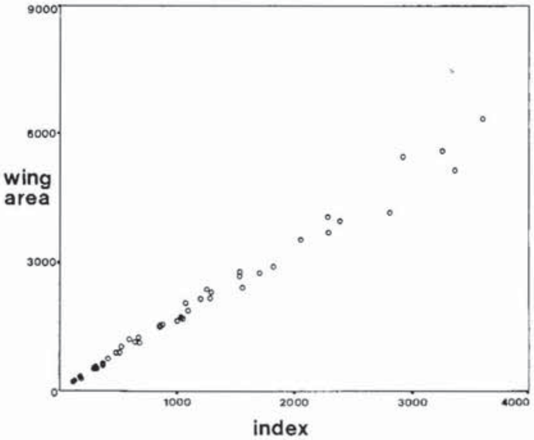

FIGURE 2

The relationship between mean wing areas and mean wing area indices for the 46 species in Table 1 for which both variables were available ($y = 1{,}665x + 35{,}820$).

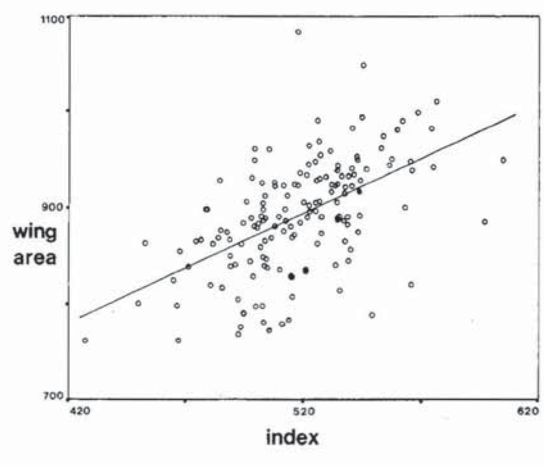

FIGURE 3

The relationship between wing areas and wing area indices for 156 Blackshouldered Kites *Elanus caeruleus* ($y = 1{,}132x + 304{,}459$).

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APPENDIX 2

The measurements used to derive correction factors applied to wing areas measured from tracings of photographs. The first column shows the number of birds measured to obtain these data. Correction factors for each species were calculated in the following way. Percentage differences (of chords) between chords and flattened measurements for wing and secondary lengths (columns 4 and 7) were added to the mean wing and secondary lengths of each species (as given in Table 1). A new wing area index was then computed from these values. The correction factor was calculated as the percentage difference between this new index and the index obtained from original wing and secondary lengths. For species where only one or two individuals were available (Table 2), this procedure was done for each bird. In the case of two birds of the same species, the average of the two correction factors was applied to the wing areas of both birds. Measurements of curved and flattened wing and secondary lengths could not be taken for several species. Correction factors for these species were taken as those of close relatives: the factor for *Falco amurensis* was taken as that calculated for *F. vespertinus*, *Aquila nipalensis* as *A. rapax*, *Hieraaetus ayresii* and *H. pennatus* as *H. spilogaster*, and *Buteo trizonatus* as *B. buteo*.

Species	Number	Wing Length Flat	Wing Length Chord	% Chord	Secondary Length Flat	Secondary Length Chord	% Chord	Correction %
F. biarmicus	5	342,2	338,8	1,0	174,6	170,4	2,5	2,9
F. chicquera	1	230,0	229,0	0,4	123,0	122,0	0,8	0,3
F. concolor	3	275,0	273,0	0,7	112,3	110,0	2,1	2,7
F. dickinsoni	4	223,5	221,8	0,8	106,8	105,0	1,6	2,2
F. naumanni	5	232,4	230,2	1,0	112,8	111,6	1,1	1,8
F. peregrinus	3	300,0	296,3	3,1	151,0	150,3	1,8	4,2
F. rupicoloides	3	265,7	263,7	0,8	140,3	136,3	3,0	4,0
F. tinnunculus	5	242,8	241,0	0,7	126,8	123,8	2,4	3,2
F. vespertinus	3	229,3	226,7	1,2	110,0	109,0	1,8	2,8
P. semitorquatus	3	114,3	113,0	1,2	75,3	73,7	2,3	3,2
T. alba	6	277,8	267,8	3,7	165,4	159,8	3,5	6,3
T. capensis	5	327,6	319,6	2,6	187,8	183,0	2,6	5,0
A. capensis	5	285,2	277,6	2,8	180,2	176,6	2,1	4,1
B. africanus	20	334,7	325,5	2,8	226,4	221,4	2,3	3,5
B. capensis	5	366,0	354,6	3,4	248,2	243,0	2,2	4,2
B. lacteus	4	441,3	435,3	1,4	302,8	295,3	2,5	3,5
G. capense	5	143,4	141,2	1,6	107,0	104,2	2,7	3,8
G. perlatum	5	106,2	104,6	1,5	86,4	84,6	2,1	3,1
O. leucotis	5	199,4	192,4	3,6	141,2	138,2	2,2	4,8
O. senegalensis	5	134,0	132,0	1,5	95,6	92,6	3,2	4,3
S. woodfordii	5	245,6	235,6	4,2	177,8	172,2	3,3	6,5
A. pomarina	1	469,0	457,0	2,6	290,0	285,0	1,8	3,7
A. rapax	5	512,6	503,0	1,9	315,2	309,4	1,9	3,0
A. verreauxi	5	602,6	597,8	0,8	405,2	401,4	0,9	1,4
A. wahlbergi	5	431,0	426,4	1,1	262,0	257,2	1,9	2,7
H. spilogaster	1	420,0	412,0	1,9	274,0	271,0	1,1	2,4
P. bellicosus	5	621,4	611,2	1,7	414,2	405,8	2,1	3,0
S. coronatus	6	473,2	462,8	2,2	371,7	363,7	2,2	3,8
L. occipitalis	5	377,2	371,2	1,6	260,4	252,6	3,1	4,4
B. augur	3	420,7	414,7	1,4	297,7	293,7	1,4	2,4
B. buteo	5	352,0	348,2	1,1	216,4	212,2	2,0	2,7
B. rufofuscus	6	413,7	406,0	1,9	280,8	275,2	2,1	3,3
C. cinereus	3	517,7	510,3	1,5	304,7	295,7	3,0	4,1
C. pectoralis	3	513,7	507,7	1,2	311,0	304,0	2,3	3,2
T. ecaudatus	3	518,6	510,6	1,6	285,0	278,0	2,5	3,6
H. vocifer	5	541,4	532,6	1,7	374,0	367,4	1,8	3,0
C. ranivorus	4	362,5	359,3	0,9	206,3	203,0	1,6	2,2
C. pygargus	2	356,0	351,5	1,3	188,0	183,5	2,5	3,5
A. cuculoides	3	300,7	297,7	1,0	183,3	179,7	2,0	2,8
M. alcinus	1	387,0	380,0	1,8	200,0	197,0	1,5	2,9
E. caeruleus	5	261,6	255,4	2,4	145,4	143,0	1,7	3,4
M. migrans	5	454,6	447,0	1,7	246,2	241,6	1,9	3,1
M. parasitus	5	411,6	406,0	1,4	227,2	220,8	2,9	4,1
P. typus	5	438,8	433,0	1,3	284,0	278,4	2,0	3,2
A. badius	5	178,2	175,6	1,5	111,8	108,4	3,1	4,2
A. melanoleucos	5	308,8	302,4	2,1	208,8	204,8	2,0	3,2
A. minullus	5	147,6	146,6	0,7	105,6	103,0	2,5	3,0
A. ovampensis	5	229,6	227,2	1,0	147,8	144,2	2,5	3,3
A. rufiventris	4	209,5	206,3	1,6	138,3	135,0	2,4	3,7
A. tachiro	5	224,0	222,6	0,6	167,8	164,0	2,3	2,0
K. monogrammicus	5	221,8	217,8	1,8	142,6	139,2	2,5	3,8
M. canorus	3	345,0	338,0	2,1	216,7	211,0	2,7	4,0
M. metabates	5	302,6	295,4	2,4	198,8	194,2	2,4	4,1
M. gabar	5	192,0	190,0	1,0	127,2	124,4	2,2	2,9
T. occipitalis	3	623,3	602,0	3,5	369,0	361,0	2,2	4,6
S. serpentarius	3	604,7	599,0	1,0	384,0	376,3	2,0	2,7