Size cline not subspeciation in the Hooded Vulture

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Abstract

Wing, tail and bill lengths of Hooded Vultures were measured on 36 wild-caught birds and 75 in museum collections. A further 60 measurements were taken from literature, and 40 measurements were received from the Musée royal de l'Afrique centrale (Tervuren, Belgium). By grouping them into regions of Africa it was shown that the smallest birds were in West Africa and the largest in southern Africa (which is well known), with a gradation in between. Sizes varied according to a cline, and were correlated with average altitude. Given that the species has the same colouration (head, caruncles, plumage) from one end of the range to the other, indeed that populations are contiguous from Senegal to South Africa, then this goes against recognising any subspecies, but rather an intraspecific trend in sizes.

Introduction

The Hooded Vulture *Necrosyrtes monachus* was originally described almost simultaneously from opposite ends of its range in Africa, from Senegal in 1823 and from the Cape Province in 1824. These first two specimens were given the names of *Cathartes monachus* Temminck 1823 and *Vultur pileatus* Burchell 1824 respectively, and for the rest of the nineteenth century they were often treated as two different species, first in the genus *Neophron* (e.g. Sharpe 1874), which also held the Egyptian Vulture *N. percnopterus*, and then by the turn of the century in the genus *Necrosyrtes* (Sharpe 1899). By the early twentieth century, however, the Hooded Vulture was said to be one species with two subspecies, the nominate *monachus* from West Africa, and *pileatus* from eastern and southern Africa (Hartert 1921, Swann 1922, Sclater 1924). It has previously been noted (Mundy *et al*. 1992: p. 136) that Burchell in 1824 did not in fact describe a Hooded Vulture but something much larger, and the first proper description of the bird in southern Africa is by Smith (1829), who named it *carunculatus*. This taxonomy has remained to the present day (Brown & Amadon 1968, Stresemann & Amadon 1979, Cramp & Simmons 1980, Brown, Urban & Newman 1982, Kemp 1994, Ferguson-Lees & Christie 2001, del Hoyo & Collar 2014, right through to Thompson *et al.* 2020).

Nevertheless, some authorities have strongly doubted the subdivision. For example, Reichenow (1900-1901) wrote "Ich kann solchen Unterschied indessen nicht finden" (translation: "However I cannot find that difference"). Bannerman (1930) doubted "whether *pileatus* should be recognised at all", and Chapin (1932) accepted two subspecies but considered that the "intergradation between *monachus* and *pileatus* is no doubt a gradual one." White (1965) agreed that there was a gradual size cline, but that "no formal division" should be made. Earlier, White (1949) had cautioned against using size alone to delimit subspecies. More recently, Brown & Amadon (1968) considered the two types as "doubtfully separable", Kemp (1994) stated that the variation was "only in size", and del Hoyo & Collar (2014) affirmed clearly that "*pileatus* differs only in size, which varies clinally, increasing from

small in W to large in E & S." Sclater & Mackworth-Praed (1919) considered the difference to be "merely that of size", and interestingly that birds from north-east Africa "agree" with the south rather than the north-west.

In addition there have been minor differences of opinion as to where the two putative subspecies meet. Cramp & Simmons (1980) and del Hoyo & Collar (2014) consider that they intergrade in Sudan, Swann (1925) that Sudan holds *pileatus*, and Brown *et al.* (1982) that it holds *monachus.* All authorities agree that the differences between the two subspecies (or from one end of the range to the other) are mainly in wing-length and bill-length but also perhaps in "longer tail and tarsi" (Ferguson-Lees & Christie 2001). No-one has suggested that there might be colour or pattern differences. From my field experience of the Hooded Vulture in northern Nigeria and in Rhodesia (now Zimbabwe), I re-examine the evidence for subspeciation in this paper. For the definition of subspecies, I use that given by Chittenden, Allan & Weiersbye (2012), where the key points are that populations are discrete in geography, and differ consistently from each other in morphology including in size.

This size difference or cline from one end of the Hooded Vulture's range to the other was well known to Gurney (1864: p. 54), one hundred and fifty years ago, who wrote that "those from South Africa being the largest, and those from the West African coast, north of the Equator, being the smallest." He maintained both ends in one and the same species, Pileated Vulture *Neophron pileatus* (Gray), over-looking Burchell. Later, Sharpe (1874) considered *pileatus* (Burchell 1824) as separate from and bigger than *monachus* (Temminck 1823); his wing-lengths were 508 mm and 470 mm respectively.

Methods

In northern Nigeria (Sokoto town) I captured seven adults by hand at their nests, and measured them. Wing length (mm) was measured from the wrist joint to the tip of the longest primary with the wing fully flattened. I believe this to be the best measure, as it gives a maximum possible length, but regretfully I have not tested its repeatability. In Zimbabwe (Rhodesia at the time of data collection) I measured the wings of 29 birds (15 adults and 14 immatures) from a larger number that I captured by cannon net. Specimens were examined in most museums of southern Africa (24) (defined here as south of the Zambezi and Kunene Rivers) and in the Natural History Museum in Tring, England (NHM) (32), and wing-lengths measured in the same way. Specimens were also measured in a few other museums, being the Muséum national d'histoire naturelle in Paris (MNHN) (11), the National Museum of Kenya in Nairobi (seven), and the Alexander König Museum in Bonn (one). Finally, by kind favour of Michel Louette I was sent wing measurements of 40 specimens from the Royal Museum for Central Africa in Tervuren, Belgium.

The literature on African vultures was searched for information, with the requirements of locality and wing length only; 60 individuals were found. Thus 211 individuals in total were measured. I included two other skins at the NHM whose wing lengths had been published: Bates (1930) quoted 485 mm for a specimen collected in Darfur by Lynes and unknowingly I measured it as 486 mm; Bates (1930) also quoted 475 mm for a bird from northern Cameroon and I measured it as 482 mm. One of the Tervuren specimens, collected at Yangambi in the then Belgian Congo, was measured at 494 mm, which earlier Louette (1988) had quoted at 498 mm. I therefore took all measurements in the literature at face value. These two birds were used from Bates (1930), one from Grant (1915), 15 from Friedmann (1930), 12 from Chapin (1932), five from Verheyen (1953), one from Rudebeck (1955), one from Aurélien (1957), and 23 from Cramp & Simmons (1980). Student's unpaired *t*-test was used to compare the means of samples.

For the large samples from southern Africa, I determined that the mean wing lengths of 15 adults (523 mm) and 14 immatures (528 mm) that were captured were statistically the same (P>0.3), and the overall mean (525 mm) was the same as for museum specimens collected from the region (n=14, mean 522 mm) (P>0.4). I therefore combined measurements from live birds and from museum specimens. I could not determine sex in the captured birds, but sex was often labelled on museum specimens. Measurements quoted by C.S. Roselaar in Cramp & Simmons (1980: p. 72) show slight differences (but not significant, P>0.1 and P>0.3 for *monachus* and *pileatus* respectively) in the means for each sex for each subspecies, amounting to females being about 2% longer in wing-length than males. Bearing in mind the number of unsexed specimens, however, the possibility of mis-sexing individuals, and this small difference between the sexes anyway, measurements for males and females in any area were combined.

Tail length was also routinely measured by me on most individuals and specimens that I handled. This was done as the length of the central rectrix from its insertion into the bird's body (pygostyle) to its tip. Occasionally the vanes were frayed but the midrib remained as a 'spike' for the measurement. Altogether 126 tails were measured.

Although bill length is often stated to differ between the two subspecies (e.g. "thinner" in *pileatus*, Ferguson-Lees & Christie 2001), it is an awkward measurement and can in fact be measured in a couple of ways. I therefore included only those measurements that I made myself, being the actual bill itself (excluding cere), diagonally from its tip to the front (distal end) of the cere (Mundy 1982: p. 17). Regretfully, some specimens in museums have the bill broken at the tip, and others were not measured, so the total sample size for the bill length was 115. I did not consider bill width or bill height.

Results

Overall, the wing-lengths of the Hooded Vulture varied from 429 mm to 555 mm (Table 1). This 29% difference is actually quite staggering; the smallest bird was an adult from "West Africa" in the NHM, and the largest an adult in the Natural History Museum (Bulawayo). The 211 individuals could be grouped into eight "populations" by geographical area; Table 1 lists these areas (with their current names), and shows the sizes in terms of the mean, standard deviation, and range (all in mm). Note that the original localities of collection are referred by me to their modern country names (see Broadley & Minshull 1986).

The mean wing length for Hooded Vultures in West Africa (Senegal to Cameroon), is the smallest at 474 mm (n=32), and significantly smaller than the means for the Sudan and north-east Democratic Republic of Congo (DRC) (P<0.05 for both comparisons). These latter two, however, are statistically the same (P>0.8), with a combined average of 484.4 mm (n=28). The mean for north-east DRC (484 mm) is smaller than that for east-central and southern DRC (497.7 mm) (P<0.001). In this last case, the collection points (Chapin 1932, Verheyen 1953) are only 600-1300 km apart.

The mean wing length for the East Africa sample (i.e. Kenya, Tanzania and Uganda) is the same as that for Ethiopia and Somalia (P=0.58), and taken together the mean for these two areas is 510.3 mm. The mean for Zambia and Malawi is statistically similar (P=0.4). The mean wing length of birds from southern Africa (definition as above) (525.6 mm) is the largest of all the geographical groups, and significantly larger (P=0.023) than that for the Zambia and Malawi group, and very significantly so compared to the two areas further to the north on the eastern side (P<0.001). The southern Africa birds show an increase of 2.3% in wing length over the Zambia and Malawi group, but an increase of 10.9% over the West African group (mean values).

Table 1. Comparison of wing lengths of 211 Hooded Vultures by eight geographical areas (see note below).

Area	Sample size	Mean wing length (mm)	Standard deviation	Range
Senegal-Cameroon	32	474.0	16.7	429-504
Sudan	12	485.0	13.3	458-501
North-east DRC[1]	16	484.0	13.1	466-520
East-central + southern DRC	32	497.7	10.2	480-517
Ethiopia + Somalia	24	511.7	14.3	485-545
East Africa (K, T, U)[2]	38	509.4	17.12	470-548
Zambia + Malawi	10	514.0	11.0	500-536
Southern Africa[3]	47	525.6	14.7	490-555

Table 2. Comparison of tail lengths of 126 Hooded Vultures by eight geographical areas (see note below).

Area	Sample size	Mean tail length (mm)	Standard deviation	Range
Senegal-Cameroon	16	222.4	10.2	210-241
Sudan	12	222.4	10.2	205-241
North-east DRC[1]	-	-	-	-
East-central + southern DRC	-	-	-	-
Ethiopia + Somalia	24	241.5	11.9	220-267
East Africa (K, T, U)[2]	19	240.0	13.9	220-261
Zambia + Malawi	9	235.8	10.1	220-251
Southern Africa[3]	46	243.0	9.6	220-265

Table 3. Comparison of bill lengths of 115 Hooded Vultures by eight geographical areas (see note below).

Area	Sample size	Mean bill length (mm)	Standard deviation	Range
Senegal-Cameroon	13	30.40	1.59	27.5-32
Sudan	9	30.00	1.10	28-31.5
North-east DRC[1]	-	-	-	-
East-central + southern DRC	4	31.25	1.89	30-34
Ethiopia + Somalia	22	30.75	1.70	28-34
East Africa (K, T, U)[2]	18	31.64	1.34	29.5-34.5
Zambia + Malawi	8	31.69	1.83	29.5-35
Southern Africa[3]	41	31.95	1.47	29-37

Notes: [1]DRC =Democratic Republic of Congo; [2]East Africa = Kenya, Tanzania, Uganda; [3]southern Africa is defined in the text as south of the Zambezi and Kunene rivers.

There is some overlap in wing lengths among Hooded Vultures from different geographical areas (Table 1). In fact, eight of 32 birds in the West African group were measured at 485 - 504 mm, and these overlapped with 6 of 24 from the Ethiopia and Somalia group, and 13 of 38 in the East Africa group, but with only two from the southern Africa group. Indeed, a bird collected at Yangambi in northern Belgian Congo (now DRC) was measured at 498 mm wing length, and was suggested as belonging to *pileatus* (Louette 1988). This amount of overlap no doubt caused Brown *et al.* (1982) to

remark that the subspecies were "not easy to separate".

Wing lengths of birds from the eight geographical areas have been recombined into six groups, according to statistical similarity, in Figure 1(a). The gradual increase in wing-length from west to east then south is clear. Figure 1(b) further combines areas from Ethiopia through to Zambia and moves southern DRC next to northern DRC; the trend is now a linear increase of about 2.73% from one area to the next.

For tail length, 126 measurements show a similar trend (Table 2), with birds in southern Africa having on average the longest tails (mean = 243 mm) and 9.2% longer than those in West Africa (mean = 222.4 mm). The average tail length of birds in the four areas in the east and south is 241.4 mm (southern Africa and Zambia + Malawi are the same, P=0.05, though border line), and 8.5% larger than the average for Sudan and West Africa. There is a spread in tail length from the shortest in the Sudan of 205 mm to the largest in Ethiopia + Somalia of 267 mm, a difference of 30.2%, very similar to the continental difference in extreme wing lengths.

For bill lengths, 115 measurements again show a similar trend (Table 3). The smallest bill length of Hooded Vultures in West Africa (27.5 mm) to the longest in southern Africa (37 mm) is an increase of 34.5%, similar to the increases in wing and tail lengths. Nevertheless, there is considerable overlap in sizes throughout the areas. On average, southern African bills are 5.1% longer than those in West Africa, a statistically significant difference ($P<0.05$).

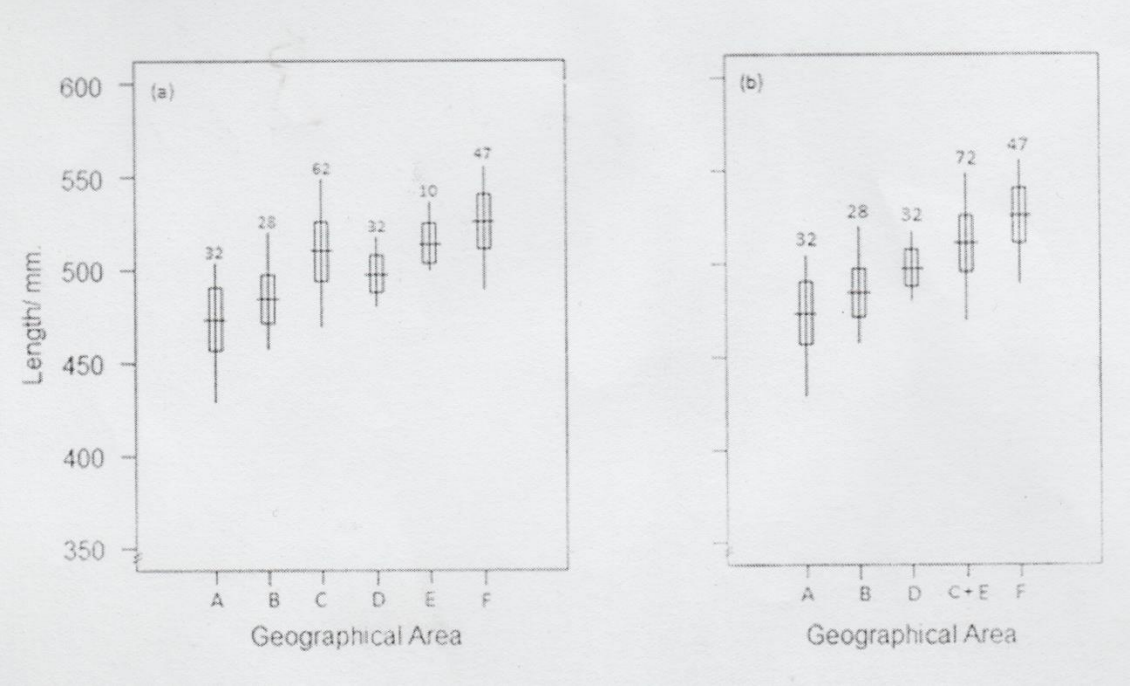

Figure 1: (a) Means, standard deviations and ranges of wing lengths of Hooded Vultures arranged in six geographical areas (see below); and (b) with some further combination of the samples and rearrangement of the areas. Numbers above the bars denote the sample sizes in each group. A = Senegal – Cameroon; B = Sudan + north-east Democratic Republic of Congo (DRC); C = Ethiopia + Somalia + East Africa (Kenya, Tanzania, Uganda); D = East-central + southern DRC; E = Zambia + Malawi; F = southern Africa (south of the Zambezi and Kunene rivers).

Discussion

The gradual and consistent increase in all measurements bespeaks of the individuals within the range of the Hooded Vulture representing a cline, or geographical gradient (Huxley 1938) in size. Whereas some birds on their wing lengths could be geographically placed, by no means can all be so placed. In addition, there is no difference in plumage colour or pattern from one end of the range to the other (pers. obs.), so that any specimen cannot be morphologically distinguished from any other by colour. (I did not check on the number of caruncles of the throat, especially on the adults, as a possibility suggested by L.J. Thompson). These two factors, size cline and colour, make an argument against the proposal of subspecies in the Hooded Vulture; no doubt, genetic evidence will also be key here.

There are two concerns with the data. While I have measured the majority of the specimens (113), nevertheless a considerable proportion (98) has been measured by other persons, indeed at least eight others. Secondly, I have combined the many fewer measurements on live birds (36 captured by me and probably 37 freshly shot from seven other persons in the literature) with 138 measurements of specimens in museums. As mentioned earlier, I have presumed that the wing lengths of Hooded Vultures (as they include the bony hand) have barely shrunk in the museums, as supported by the statistical test. In brief, and with some justification, all the measurements have been taken at face value. I should however note in passing that some of the specimens are very old. For example, several in the Natural History Museum at Tring were collected in the 19th century. Perhaps the oldest in that museum was collected in 1851 (I measured it in 1976), while the oldest in the MNHN at Paris pre-dates it at 1832 (I measured it in 1999). I have also accepted any locality data as written on the labels of museum specimens, though realising that there can sometimes be a problem with these (e.g. Rasmussen & Prŷs-Jones 2003).

To a great extent, this size cline in the Hooded Vulture is correlated with the topography of the African continent. A curved line from Port Sudan in the north, along the western side of the western arm of the Great Rift, east and south of the Congo basin with its great rain forest, and westwards to Luanda in Angola, divides Africa into Low and High (Moreau 1966: pp. 13-14, Fullard & Darby 1967: pp. 116-117, Grove 1978: p. 1). Most of Low Africa, to the north and west of this line, has an altitude below 600 m a.s.l., whilst High Africa to the east and south has an altitude mostly above 1000 m a.s.l. The smallest Hooded Vultures, in terms of wing lengths at least, are in Low Africa, Senegal to Sudan and northern DRC. Bigger vultures are in High Africa. Soaring vultures perhaps 'need' larger wings at the higher altitudes in order to extract the same amount of lift in the more 'rarefied' atmosphere. This is not necessarily the same as being subject to Bergman's 'rule' on body size which has to do with ambient temperature (re-phrased in Blackburn, Gaston & Loder 1999). I expect, however, that body mass in these vultures is in fact positively correlated with their wing lengths. From my own measurements, eight captured adults in northern Nigeria weighed on average 1.69 kg and had wing lengths averaging 475 mm, whereas 19 adults captured in Zimbabwe (Rhodesia at the time of data collection) averaged 2.17 kg and the wing lengths averaged 523 mm. Due to the paucity of data on weights in the literature, I have no more data on this correlation. A second likely factor influencing the cline is the latitudinal 'rule', whereby within a species individuals are larger the further they are located from the Equator (Blackburn *et al.* 1999). The Hooded Vultures in the area of southern Africa are south of 16°S, and in the 19th century (but not now) they were located as far south as 30°S. They could not reach that latitude in North and West Africa due

to the Sahara Desert. Hamilton (1961) has exhaustively discussed the likely selection forces acting on a species that shows an intraspecific trend in wing length. There is likely to be "more than one selection force" operating (*op. cit.*: p. 188), though "pressure of air" (p. 185) was one.

For the purposes of my analysis, I have divided up sub-Saharan Africa into eight regions based to some degree on statistical similarity in the wing lengths of Hooded Vultures. In a fascinating exercise, Linder *et al*. (2012) partitioned sub-Saharan Africa into seven regions, though with barely a mention of altitude. Their Figure 2 drawn from the "combined matrix" of using all five taxonomic groups, fairly well follows High and Low Africa. Nevertheless my regions do not strictly follow theirs; but this difference could be expected from a wide-ranging vulture (Thompson *et al*. 2020).

The biggest difference in wing lengths between neighbouring areas is that from Sudan, at an average of 485 mm and an altitude of about 500 m, and Ethiopia, at nearly 512 mm and an altitude of over 1000 m. This sudden increase seems to occur within a short distance of only 200 km, and appears to contradict the progression of a cline. It remains as something of an anomaly, which should be investigated further and in more detail. Ethiopia is known as the 'roof of Africa' and has sharp escarpments to the west (Sudan) and to the east (Afar country). Given that the locality data are correct, the anomaly suggests that Sudan's Hooded Vultures stay in Sudan (and South Sudan) and Ethiopia's Hooded Vultures stay in that country. Indeed, when the cline is fragmented along its length into geographical areas, the overall suggestion is that birds remain true to their natal zone, demonstrating site fidelity. For species as presumably wide-ranging as vultures, this phenomenon too is curious; the Hooded Vulture, which occurs throughout most of sub-Saharan savanna Africa (Mundy *et al*. 1992: p. 139), is not a free-mixing (i.e. panmictic) species, but it prefers its own neighbourhoods.

This is the basis of a third concern with the data. At whatever locality a bird is captured or collected, and subsequently measured, it cannot be known where in fact the individual 'belongs', unless it is at its nest. This has the effect of 'blurring' the differences. That is to say, a larger Ethiopian bird could presumably be collected in the Sudan and *vice versa*. Wandering movements of vultures will contribute to the overlaps among areas.

The overall result, of a cline in size from West to East to southern Africa, is the same as that for another small vulture in Africa, the Palm-nut Vulture *Gypohierax angolensis* (Donnelly & Irwin 1972). In that species the wing lengths ranged from 386 mm in West Africa to 466 mm in eastern and southern Africa, on average being about 18% shorter than for the Hooded Vulture. Those authors said that the reason for the cline was "not clear", but that the increasing size did follow the "diminution of rainfall eastwards". Palm-nut Vultures are forest birds, Hooded Vultures are mostly savanna birds (Mundy *et al.* 1992: p. 139, p. 224), and (the lower) rainfall is unlikely to be the driver for the cline in the latter, though aridity is listed by Hamilton (1961). It remains to be seen whether this effect of altitude and latitude on wing length is duplicated in other species of sub-Saharan African vultures and indeed, in New World (Cathartidae) vultures too. In fact the Turkey Vulture *Cathartes aura* of the Americas offers an interesting comparison. Up to six subspecies have been described on "poorly defined" size and colour differences (Kirk & Mossman 1998: p. 3). There are migratory and sedentary populations living throughout North and South America, and an island population (*C. a. falklandica*), but it is not yet clear how the intraspecific trends in wing, tail and colouration may define subspecies or otherwise. Wetmore (1964) measured 227 museum specimens (without stating the method), and among the six putative

subspecies there was considerable overlap in the ranges of wing lengths (at least), as with Hooded Vultures here (Table 1). Suffice to say for the present, that Hooded Vultures in Africa exhibit a cline in size.

Meanwhile some preliminary results of genetic analysis so far show West and South African Hooded Vultures as being genetically distinct (Anon. 2018).

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