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Factors Influencing the Timing of Breeding in African Vultures

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Most birds have a clearly defined breeding season. In temperate regions almost all birds breed during the summer, when warm weather, long days and increased food supplies combine to produce the best conditions for rearing young. But for many tropical species there may not be such a combination of advantages to any one season, and birds could breed in any month of the year. The factors which influence the timing of breeding have been well studied in passerines (Perrins 1970) and some tropical seabirds (Harris 1969), but birds of prey have received little attention (see review by Newton 1979). In this paper I consider the information available for African vultures to see whether it indicates which factors influence breeding. I have come to no firm conclusions, except that the determination of breeding in these birds may be complex and variable.

Most vulture species are exclusive scavengers. They rely on finding carrion and do not normally kill prey. Nine species occur in Africa, south of the Sahara. Apart from the Lammergeier *Gypaetus barbatus*, which lives in mountains, all species live in savanna and semi-desert areas where they feed mostly on carcasses of large ungulates. Up to six species may be seen at any one carcass, feeding specialisations reducing competition between them (Kruuk 1967; Houston 1967a). A popular misconception is that vultures feed on remains of predator kills. In fact, most predators consume virtually all the food from a kill before they abandon it, and vultures obtain an insignificant amount of food from this source (Houston 1979). But predators account for only a small proportion of ungulate mortality, and in migratory populations most individuals die from such factors as malnutrition, disease, parasites or accidents. When these animals die, the majority are located by vultures, who then congregate rapidly and consume the meat before any of the mammalian scavengers have time to compete (Houston 1979). It therefore follows that the food supply of vultures in natural ecosystems is closely associated with ungulate mortality. All savanna regions of Africa have a highly seasonal climate, determined by alternating wet and dry seasons. The quality of grazing available for ungulates varies greatly between these, and is particularly bad at the end of the dry season; this is when ungulates are found in poor condition, and when their mortality is greatest (Sinclair 1977). The food supply for vultures is, therefore, highly seasonal and the peak of food abundance comes at the end of the dry season.

Vultures have two advantages over other raptors when one wishes to study the factors involved in the timing of breeding. Firstly, several species coexist together, all tapping the same food source and hence, presumably, subject to the same variations in supply. These species do, however, vary in body weight from under 2kg to over 9kg, and the lengths of their incubation and rearing periods differ by several months. A comparison between species might therefore indicate if there is any stage in the breeding cycle which is timed to coincide with periods of high food availability, for we would expect that part of the breeding season to occur at the same time of year in all species, irrespective of the overall duration of their cycles. Secondly, because vultures feed on carrion, their food supply can be quantified in a way that is difficult for most other birds of prey. For the majority of predatory species it is hard to know when food is most available, for prey may be abundant at one season yet difficult to catch, but scarce at another and easily caught. Because vultures feed from large mammal carcasses there is no seasonal change in prey catchability, and the overall size of their food supply can be quantified from ungulate mortality data.

The first question to establish is whether vulture species show any breeding synchrony and if there are clearly defined breeding seasons. Some tropical birds do not have annual cycles, such as some seabirds which breed every 8-10 months. In certain species, like Sooty Terns *Sterna fuscata*, there is close synchrony among individuals, but in others, such as Brindled Terns *Sterna anaethetus*, egg-laying may occur in almost any month. This arises probably because the food supply for these species is more or less constant through the year, so there is no advantage to breeding at any particular time. Such birds appear to start each breeding attempt as soon as they have been able to complete the moult after the last breeding season, and this results in breeding intervals of less, or in some species more, than twelve months.

At least one tropical raptor, the Galapagos Hawk *Buteo galapagoensis*, has no synchrony and birds can be found at various stages of breeding throughout the year (De Vries 1975). For vultures the only long-term information comes from some colonies of Cape Vultures *Gyps coprotheres* in South Africa which have been observed for about forty years. Mundy (1982) gives detailed laying dates for three of those years and clearly illustrates the definite breeding season which one colony has maintained over the years. Detailed studies have so far been made on six species of African vultures, all of which have a clearly defined, annual breeding season.

In considering this timing, it is helpful to distinguish between 'ultimate' and 'proximate' causal factors, as proposed by Baker (1938). The ultimate factors are those which influence survival, and which through natural selection determine the best season for breeding. For example, if food is most abundant at one season, and birds which breed at that season give rise to a larger number of surviving young, then through natural selection that season of the year will become established as the breeding season; the food supply here acts as the ultimate factor. This may be quite distinct from the factors which initiate breeding and are termed proximate factors. For example, in order to have the young in the nest during the season when food is abundant, a bird may need to lay the eggs several months previously, when food conditions are poor. The bird therefore needs to have some cue to initiate breeding at an appropriate date before conditions are optimal. These factors are called proximate, and may be daylength, rainfall or some other factor which influences the phsyiology and behaviour of the bird.

I will not consider proximate factors here. Of the ultimate factors which have been proposed as being likely to influence breeding in birds, some aspect of the food supply is probably the most important. The only other factor which has been suggested for birds is predation, for in some species which suffer a heavy predation when nesting, there may be an advantage to individuals in synchronising their breeding and thus 'swamping' any potential predators. This factor might concentrate breeding in one season, but food supply is still likely to influence the choice of that season. However, predation is not a factor that is likely to influence vulture breeding, because the birds have few predators. I am therefore assuming that some aspect of food supply is the ultimate factor determining the timing of breeding in vultures.

There are three periods during the breeding cycle when birds could be influenced by the availability of food: firstly, the time of egg production and incubation; secondly, during the growth of the chick; and finally, when the young leave the nest. I will consider each of these stages in turn, using information from the Serengeti region of northern Tanzania in the early 1970s. The data were from 84 nests of Rüppells Griffon, 74 of White-backed Vulture, 63 of Lappet-faced Vulture, 5 of White-headed Vulture and 3 of Hooded Vulture. The small sample sizes for the last two species make their contribution rather speculative, but for both species there is confirmatory information from many more nests studied in less detail.

1) Timing of egg laying: In some small passerines, many females are unable to lay as early as they need because they are unable to obtain sufficient food to form the eggs (Perrins 1970). Such species appear to lay as soon as the female is able to obtain sufficient additional food above that required for normal maintenance. The timing of the breeding season is therefore, for these species, determined by the rise in food supply after the winter, and birds start laying as soon as sufficient food becomes available. The same may be true in Sparrowhawks *Accipiter nisus*, for an experimen-

tal increase in their food supply in spring resulted in larger clutches and, sometimes, in earlier egg laying (Newton & Marquiss 1981). If this situation applied to the vultures, then all species should lay at the same time, because they share the same food supply. Egg production by a female vulture represents only 3-9% of her total body weight (Table 1), and is not therefore comparable with the egg production of a small passerine, which may exceed the total body weight of the female (Perrins 1970). However, the female also has to accumulate sufficient body reserves to withstand long incubation stints. These reserves are far more substantial than those needed for egg production and their accumulation is more likely to influence the timing of laying than egg formation itself (Newton 1979).

Table 1. Egg and body weights for some African Vulture species.

Species	Egg weight[a] g	Body weight[b] kg	Egg weight as proportion of body weight
Rüppell's Griffon *Gyps rüppellii*	233	7.4	3.1%
Cape Griffon *Gyps coprotheres*	240	7.7[c]	3.1%
White-backed Griffon *Gyps africanus*	214	5.3	4.0%
Lappet-faced Vulture *Torgos tracheliotus*	240	6.2	3.9%
White-headed Vulture *Trigonoceps occipitalis*	196	4.0	4.9%
Hooded Vulture *Necrosyrtes monachus*	122	1.9	6.4%

Figure 1 shows the laying dates for five vulture species in the same region. They differ considerably, so provide no evidence that food supply influences the timing of laying in all five species.

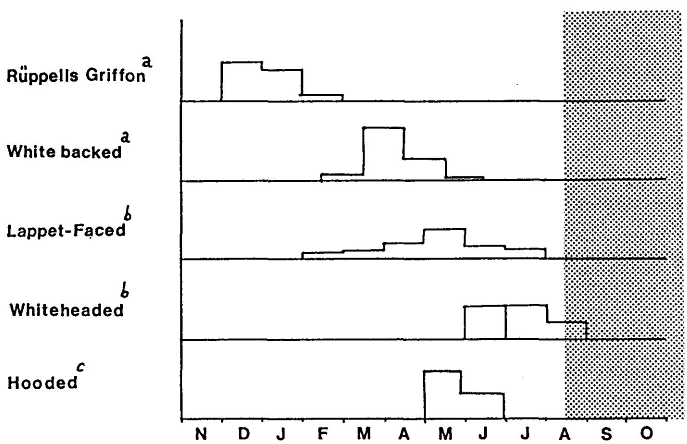

Figure 1. Laying dates for vulture species in the Serengeti region of northern Tanzania, showing for each species the percentage of eggs laid in each month. The hatched area indicates the end of the dry season in this region, which is when the food supply for vultures is most abundant. Data from a Houston 1976b, b Pennycuick 1976 and c Houston (unpublished).

This may seem a rather simplistic test of whether food for egg formation acts as an ultimate factor, for two reasons. Firstly, the different vulture species show a dominance hierarchy in which some species are dominant over others (the usual dominance hierarchy is Lappet-faced Vulture - Rüppell's Griffon - White-backed Vulture - Hooded Vulture). We might therefore expect that, if food supply determines the date of egg laying, the dominant species would reach the threshold at which they start laying some weeks before the subordinate species. However, Figure 1 shows no convincing evidence to support this. Secondly, the species also vary in the extent to which they depend on large mammal carcasses. Lappet-faced, White-headed and Hooded Vultures probably obtain some food from other sources, and kill some prey themselves; also they do not depend entirely on communal feeding parties with other vultures (Houston 1976a). They may therefore have a slightly larger food supply and, if the date of egg laying was determined by food intake, might be expected to breed earlier. But these species are actually the last to lay.

In conclusion, this interspecies comparison does not imply that food availability determines the timing of laying.

2) The second critical period in the breeding season could be the time when the food requirements of the chick are at their greatest. If vultures time their breeding season so that young are in the nest during the period of maximum food availability, we would predict that all species would have rapidly growing chicks in the nest at the same time of year, and that this would be the season of maximum food availability.

For Rüppell's and White-backed Vultures, the food requirements of the young have been determined by hand-rearing young birds and recording the daily intake. This was shown to reach a peak about half-way through the nestling period, when chicks ate more than twice as much as adults (Houston 1976). The time of peak chick growth does therefore impose demands on the adults.

Since other vulture species have similar growth curves, they probably also have peak food requirements about half-way through the nesting period. Figure 2 shows the period when the daily food intake of the young of various vulture species is expected to be greatest. These periods are not synchronised between species, suggesting that food requirements at this stage are not determining the timing of breeding.

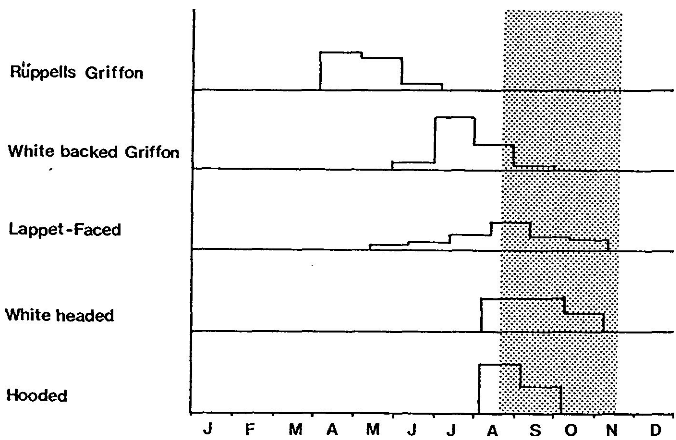

Figure 2. Dates during the rearing period of various vulture species when the food requirements of the chick would be expected to be greatest, showing for each species the percentage of nests at this stage in each month.

We would, however, expect close synchrony only if the food supply was limiting and there was only one brief period of a few weeks when sufficient food was available to provide for the additional demands of the chicks. This might not be the case, and although food is most abundant at the end of the dry season, there may still be sufficient food throughout the dry season to enable birds to rear young. There would then be no advantage in synchronising the rearing period. However, the amount of food required during the breeding season by a Rüppell's Vulture was considerably greater than the amount that breeding birds were able to obtain. During the second half of the nesting season the adult birds lost most of the fat they had laid down prior to breeding (Houston 1976b). It therefore seems that Rüppell's Vultures were rearing young during a season when food was insufficient to supply both adults and chicks.

To conclude, the availability of food for the period of rearing the chick is not the ultimate factor determining the timing of breeding in Rüppell's Vultures. The other vulture species have their young in the nest later in the dry season, and may take advantage of the greater food supply at this time of year.

3) The third stage in the breeding cycle which might be influenced by food availability is the period when the young chick becomes independent of its parents. A nesting attempt is only successful if it gives rise to a young bird which subsequently survives. Young vultures face considerable hazards when they try to leave the nest. Most vulture species do not feed their young away from the nest, and so once a young bird starts feeding for itself, it will face competition from older, more experienced birds at carcasses. Young birds are less aggressive than adults (Houston 1976b). Moreover, the level of aggression in vultures is partly determined by their degree of hunger (Valverde 1959). It therefore follows that a young bird is likely to stand a better chance of survival if it leaves the nest during a period of food abundance, when there will be reduced competition for food from adult birds. Vultures might time their breeding season so that the young leave the nest at the end of the dry season, so that the young will stand a good chance of survival. The data in Figure 3 show the season when the young of the various vulture species are finally leaving the nest. This estimate does provide the closest synchrony between species and it is clear that all species release their young towards the end of the dry season.

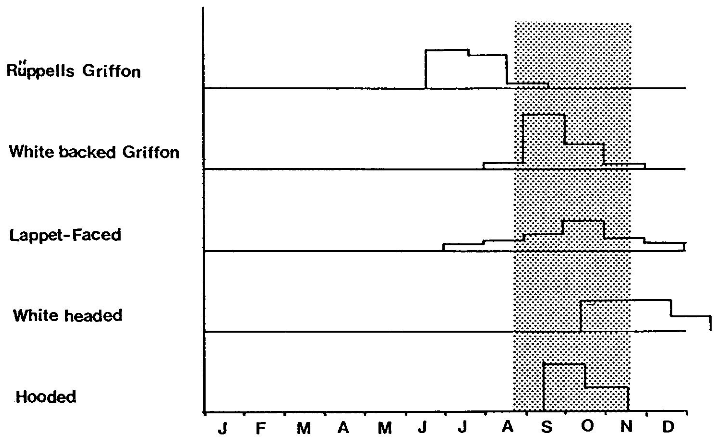

Figure 3. Dates at which the various vulture species have chicks leaving the nest, showing for each species the percentage of young at this stage in each month.

However, there is an unknown period of time between when the young bird first leaves the nest and when it becomes completely independent. Young vultures often return to their nest sites for several months after fledging, when they may be fed by their parents. There is great variation in the length of time which parents are prepared to feed their young in this way, both between species and between individuals of the same species (Mundy 1982; Robertson 1983). It is not known how important this post-fledging parental feeding is for the young birds and whether it represents a significant part of their diet. Because there is little information, it is not possible to plot the time at which young become totally independent of their parents, which would be a better test of the influence of food availability on the timing of breeding than the date of first flight. It is, however, still reasonable to assume that there would be strong selective pressure on the adults to shorten the length of time for which they have to provide food for the young after fledging, and also remain at the nest site after the young have left. These might be additional factors that would favour the timing of breeding such that young first left the nest at a season when food was abundant enough for them to become independent of the adults in a short period of time.

We might therefore conclude, on the evidence from the Serengeti region in the early 1970s, that the ultimate factor influencing the timing of breeding is the availability of food when the young leave the nest, and not the food required for rearing the chick or for egg formation.

How does this compare with other regions? In Africa the rainy season is determined by the movement of a rain belt, which moves north and south of the equator, largely due to the movement of the inter-tropical convergence zone. In consequence the end of the dry season does not occur at the same month in different parts of the continent. For example, in the Sudan it occurs in April, while in Zambia in November. If the breeding season of vultures was ultimately determined by the need to release young at the end of the dry season, we would predict that, if we examined the same species in different parts of Africa, laying would occur in different months, but there would be a constant time interval between laying date and the end of the dry season. The only species for which there is sufficient information to enable this comparison to be made are the large, cliff-nesting Rüppell's and Cape Griffon Vultures, which have almost identical lengths to their breeding seasons. Figure 4 shows that, from information available on laying dates in the literature, there is not the clear relationship that we would expect. In other parts of Africa birds cannot, therefore, be timing their breeding in order to release young from the nest at the end of the dry season, as we suggested for the Serengeti. This implies that the timing of laying may vary with locality, irrespective of seasonal factors.

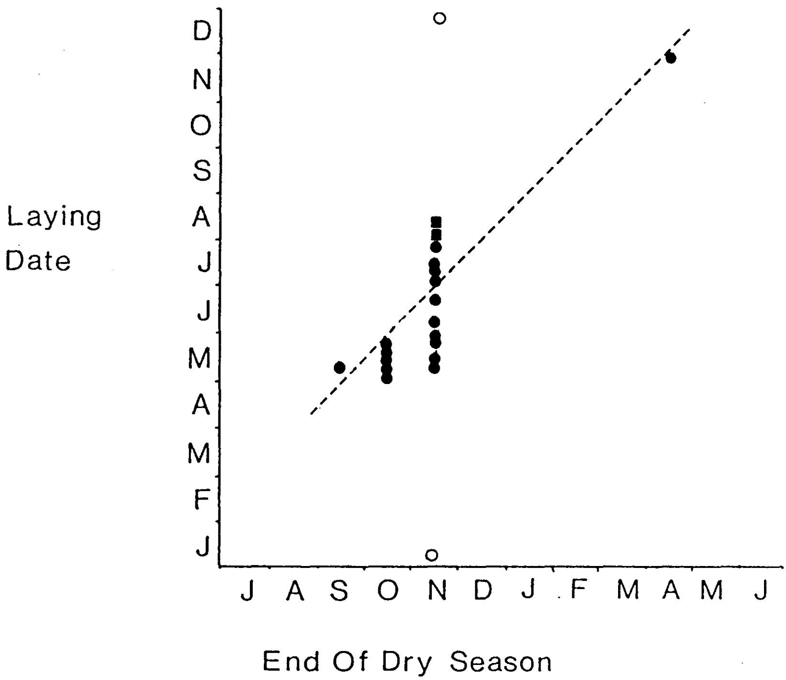

Figure 4. A comparison from different parts of Africa of the month of peak egg laying of Rüppell's and Cape Griffon Vultures and the month at which the dry season usually ends. Data on vulture breeding seasons from Benson (1945), Houston (1976b), Irwin (1981), Mundy (1982), Robertson (1983) and Vernon *et al.* (1982, 1986), and data on rainfall from Thompson (1965). Breeding data for the Serengeti colonies in 1985 and 1986 are shown as ■, and these figures have been used instead of the dates from Houston (1876b, shown as ○) to form the correlation given in the text.

As a further complication, the Rüppell's Griffons in the Serengeti have changed the timing of their breeding season during the last fifteen years. In the early 1970s this series of colonies, which may contain 1,500 to 3,000 nests (Pennycuick 1983), had a clearly defined laying period in December/January. In the 1985/86 season, birds in the same colonies were laying in August (Houston, in prep.). A shift in the breeding season on this scale is most remarkable; it is the only known case of any species of raptor with a synchronised annual breeding season changing the whole timing of that season. It is not clear why this should have occurred, although it is probably associated with the increase in the food supply in the area (calculations of the food available to vultures suggest a substantial rise during the last fifteen years). If the laying dates of the 1985/86 seasons for these colonies are used in place of those from the early 1970s in the comparison between breeding date and the end of the dry season (as in Figure 4), they result in a significant correlation ($r_s 19=0.68$, $p > 0.01$). In this situation the eggs are laid, on average, four and a half months before the end of the dry season. The incubation period is about 55 days, so that the young will be about half-way through their period of dependence on the adults at the end of the dry season.

It therefore appears that at least one vulture species is able to alter the timing of its breeding season. Nothing is known about the proximate factors which initiate breeding in vultures, but the fact that such a change can occur means that any seasonal variable such as daylength or rainfall cannot be wholly responsible. Presumably there is some interaction between the nutritional state of the birds and their hormone balance which results in birds coming into breeding condition at different times of the year in different feeding conditions. Perhaps, in conditions of relative food abundance, vultures time their breeding so that the young are in the nest during the end of the dry season, when food is most available. This is the typical pattern found in other bird species. But maybe when there are relatively poor food conditions, they rear their young much earlier in the year, to ensure that the chicks fledge during the end of the dry season. Clearly the timing of the breeding season in vultures is more complex than it at first seems.

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