THE BREEDING PERFORMANCE OF WILD HELMETED GUINEAFOWL (*NUMIDA MELEAGRIS GALEATA* PALLAS) IN THE WAZA NATIONAL PARK, NORTH CAMEROON

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INTRODUCTION

For the description of the population dynamics of a group of individuals, one needs information on density, mortality and recruitment as well as on immigration and emigration (Lack, 1954 ; Von Haartman, 1971 ; Ricklefs, 1973 ; Eberhardt 1985 ; Clobert & Lebreton 1991). The biological significance of these demographic parameters is determined by species studied, the population studied and the methodology used (Clobert & Lebreton, 1991).

The Helmeted Guineafowl (*Numida meleagris galeata* Pallas 1767) is a characteristic member of the African savanna avifauna (Chapin, 1932 ; Crowe, 1978). Its wide distribution is partly due to the adaptation of this bird to varying ecological conditions. These include both physiological and morphological adaptations (Crowe, 1978). In nature, the species breeds only once a year throughout its geographical distribution. Another important biological characteristic of the Guineafowl is its high egg production : 15 to 20 eggs per clutch in the wild (Ayeni, 1980) and 40 to 100 eggs produced per female per year in improved stocks (MacCarthy, 1974 ; Chrappa *et al.,* 1978).

In birds, the breeding of females and the subsequent growth of young seem to depend on the acquisition of high-protein food (Davis, 1943 ; Jones & Ward,1976 ; Woodall, 1994). Climatic factors are also known to influence breeding success in birds (Liversidge, 1966, 1970 ; Syroechkovskiy *et al.,* 1991 ; Telleria & Diaz, 1995). It has been suggested that rainfall influences breeding success in guineafowl through the availability of protein-rich insect food (Mentis *et al.,* 1975 ; Crowe, 1978). There are also reports that reproduction in guineafowl is governed by the combined effect of relative humidity, temperature and number of hours of sunshine together with rainfall (Onuora, 1983 ; Crowe, 1978).

Studies in Nigeria by Aire *et al.* (1979), Ayeni (1980) and Onuora (1983) have shown that breeding in wild Helmeted Guineafowl only occurs during the rainy season. Barbier & Leroy (1970) also reported that spermatogenesis in the Guineafowl begins in April, reaches its peak between May and August before

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decreasing to the resting stage between September and November. However, eggs with very low fertility can be laid during off season periods (Ayorinde, 1987). Factors like age of the bird (Veitsman & Pavlova, 1972 ; Martin, 1995), sex ratio (Veicman, 1962 ; Gonzalez & Klein, 1974), nutrition (Offiong & Abed, 1980 ; Offiong, 1983 ; Monaghan *et al.,* 1992) and predation (Greenwood *et al.,* 1995) might influence the breeding performance in birds too.

On the basis of these informations, it was hypothesized that the breeding performance of the Guineafowl in the Waza region, which has an unpredictable and fluctuating annual rainfall, will vary from year to year due to variations in environmental conditions. In this context, the following research questions were asked :

1 - What are the major factors influencing breeding success in wild guineafowl in the Waza region ?

2 - To what extent do these factors influence breeding success of individuals in this population ?

3 - What are the recruitment rates under these conditions ?

METHODS

THE STUDY AREA

The study area covers about 100 hectares in the western part of the Waza National Park in Northern Cameroon. The terrain is gently undulating, with an average altitude of about 307 metres. Yearly maximum temperature is around 40 °C and the minimum is around 18 °C. The hottest month is April (average temperature 32.8 °C) and the coldest is January (average temperature 26.1 °C). There are two main seasons, a rainy season from May to October and a dry season from November to April. Rainfall varies from 500 to 800 mm per year. The vegetation of this region was described by Wit (1975) and recently by Gaston (1991) and is of a Sudan-Sahelian type.

DATA COLLECTION

Start of the breeding season and clutch size

During the 1992, 1993 and 1994 guineafowl breeding seasons, a search team of 4 people went out in search for nests. The searchers were spaced 100 metres apart, and moved in the same direction looking out for nests and using a compass to keep course. A stick of about 1 to 1.5 metres long was used to separate tall bushes apart. Each search session (only one per day) lasted for 4 hours during the morning period, with a 10 minute break each hour. This was because previous experience showed that after a long search, some members of the search team lost concentration, increasing chances of missing nests.

Data collected included those from females tagged earlier for home range studies (6 radio-tagged and 77 ring-tagged) and those from untagged birds. The tagged birds permitted observations on re-nesting and the comparison between nest success of first and of experienced breeders. When nests were found, the characteristics of the nest sites, height and type of vegetation under which nest was found, height and nature of surrounding vegetation, were noted. The identity of the bird if tagged, was determined from the ring colour or from the radio frequency with a Biotrack Mariner 57 receiver. The number of eggs (if any) was noted and the geographical location was determined using a Magellan Geographical Positioning System (GPS), to facilitate future localisation. After finding, the nests were then revisited once a week till hatching or till it was clear that it had been abandoned or preyed upon.

Since frequent nest visits may disturb breeding birds (Mayfield, 1975 ; Johnson, 1979), a one week visiting interval during the laying stage and once a day during the late incubation stage was assumed to be sufficiently long to avoid interference with nesting hens. Subsequent data on nests were collected at a distance of about 5 to 10 metres from the nest, in order to minimise the chances of human interference with the breeding. Changes in the clutch size were recorded on each visit till hatching or loss of the nest.

Calculation of breeding index

A breeding index (I) for each year was calculated by assuming that the number of nests found by our search team (which was made up of the same people for all the years) was an index of the breeding intensity (or nest density) for that year. I also assumed that the probability of finding a nest was the same for all nests and for all searchers. If N is the number of nests found in a month by a number of people, X, searching for a number of days, Z, the breeding index, I, for that month was calculated using the formula $I = N/XZ$.

« Search effort » was the product of the number of searchers and the number of search days. The breeding index was thus expressed as the number of nests found per search effort. One person searching the study area for 4 hours (= 1 day) was said to have exerted one unit of search effort. Nests without eggs were not used in the calculations. The breeding index for each year was then calculated as the geometric mean of the breeding indices for the breeding months for that year.

Calculation of nest survival

To overcome bias that usually result from the calculation of nesting success as a simple percentage of hatching from a sample of nests found independent from the time period that the nest is under study, Mayfield (1961, 1975) proposed an alternative method that takes into account nests found or lost at different stages of incubation. He measured the nesting success as a daily survival rate, which he defined as the probability, P, that a nest will survive from one day to the next. This was calculated from the formula $P = F/F + L$, where F is the total number of « nest days » (the sum of all daily totals of nest present during the observation period), and L is the number of nests lost. If a nest was lost in-between two field visits, he assumed that the nest was lost halfway between the visits. If t1, t2 and t3 are the total number of days of laying, incubation and nestling respectively and P_l, P_i and P_n are the probabilities of nest surviving from one day to the next during the laying, incubation and nestling stages respectively, the nest survival for the whole laying period will be given by P_l^{t1}, nest survival for the whole incubation period by

P_i^{t2}, and nest survival for the whole nestling period by P_n^{t3}. The survival from the start of laying till fledging, P_{total}, (= recruitment), will be given by the product of the survival during the laying, incubation and nestling stages, ($= P_l^{t1} \times P_i^{t2} \times P_n^{t3}$).

Daily survival rate as well as survival during the laying, incubation and nestling stages were calculated using Mayfield's formula. The standard errors for the results were calculated using the formula derived by Johnson (1979) and is :

$$S.E. = \sqrt{\frac{L(F-L)}{F^3}}.$$

The 95 % confidence limit was calculated as 1.96 × S.E. Hatching success was calculated as the percentage of eggs present before hatching that effectively hatched into young. A Spearman rank correlation was used to compare differences in clutch size between first and experienced breeders. A multiple regression test was used to compute the relationship between clutch size, nest loss and breeding success.

Causes of nest loss

Causes of nest loss were determined by direct observation of lost nests. For preyed nest, the predators were identified by direct observation of foot-prints around the nest. Earlier observations showed that the manner in which egg shells were scattered around preyed nests was typical for each predator species and this feature was also used to identify some nest predators.

Influence of food availability

To verify how food available to the Guineafowl varies during the study period and how this could influence breeding, insect and seed abundances were estimated monthly. Crawling insect abundance was estimated by using 100 aluminium cup traps buried in the ground with the opened end just at ground level. The cups were arranged in rows of 5 per site. Each row was separated by 500 m from the next. A total of 6 randomly selected sites were chosen for this investigation. Four sites were chosen in the National Park, and two outside. The traps were set around 5.30 h and collected around 18.00 h The number of insects in each trap was noted.

Seed abundance was estimated in the same sites as those for the insect abundance estimate. The topmost 2 to 5 cm of soil (accessible to the birds) were collected in one square metre quadrates placed at 100 metres apart and 10 per site. These soil samples were brought to the field station, each thoroughly mixed, and 100 g sub-samples were taken for investigation under a microscope at 10X magnification. All the seeds in each soil sample were counted.

Influence of rainfall

Rainfall data were collected from the National meteorological Station in Waza for the three research years. A simple regression of the yearly breeding success on the total annual rainfall figures was carried out.

RESULTS

START OF BREEDING AND CLUTCH SIZE

Pairing started by early March, just after the first rains in all three years. Egg laying started by early August each year. The breeding season for all three years lasted for about two months, with maximum egg production between mid-August and early-September. The form and shape of guineafowl nests are described in Ayeni (1980). Up to 67 (76 %, N = 88) nests were located under scrubs of between 1 and 3 meters tall. Of the remaining 13, 7 (8 %) were found under isolated tuffs of grass of height ranging between 1 and 3 metres and 6 (7 %) in the open. Up to 71 (81 %) of the nest sites had very open surrounding (average grass height < 2 m). No nest was found in very thick bushes or under big trees.

The clutch size varied from 1 to 22 eggs. Mean clutch size for all three years for all nests found (± 95 % confidence limits) was between 7.9 ± 3.1 and 10.2 ± 5.0 eggs. Successful nests generally had higher clutch size than unsuccessful ones for all three years (P < 0.05, N = 88). The mean clutch size of successful nests for the 3 years was between 11.6 ± 3.6 and 13.1 ± 2.4 eggs. Table I summarises the mean clutch sizes for all three years. The breeding index (I) was higher for 1994, 2.22 than for 1992 and 1993, 1.19 and 1.16 nest per search effort, respectively.

TABLE I

Mean clutch size for first-time and experienced breeding guineafowl hens.

	Year	mean clutch size ± 95 % confidence limits		Overall mean ± 95 % confidence limits
		First time breeders	Older breeders	
All nests	1992	7.3 ± 4.7	11.5 ± 3.9	9.4 ± 4.3
	1993	5.4 ± 3.7	10.4 ± 3.1	7.4 ± 3.1
	1994	8.3 ± 5.9	12.1 ± 4.1	10.2 ± 5.0
Successful nests	1992	9.0 ± 3.0	15.8 ± 1.0	12.4 ± 2.0
	1993	—	11.6 ± 3.6	11.6 ± 3.6
	1994	9.8 ± 2.7	16.4 ± 2.1	13.1 ± 1.0

CAUSES OF NEST LOSS

The magnitude of each factor responsible for nest lost varied with year and breeding stage (Table II). Four main factors were identified which accounted for the total of the losses during the laying stage for the 3 years, nest abandonment 39.0 % (n = 16), predation 24.4 % (n = 10), flooding 19.5 % (n = 8) and trampling by elephants 17.1 % (n = 7).

During incubation, predation was the dominant factor responsible for nest loss, accounting for up to 90.4 % (n = 19) of losses at this stage for all three years, and 100 % (n = 5) in 1994. Other factors of nest loss at this stage (observed only in 1992 and 1994) were nest abandonment and trampling by elephants accounting for 4.8 % (n = 1) of nest loss each. No nest was lost during the nestling stage during the three research years.

Most of the nests lost through predation (76.0 %, N = 29) were completely destroyed, and in two cases the hen guineafowl was also eaten. The most

TABLE II

Variations and magnitude of factors causing guineafowl nest loss.

Year	number of nests lost	Factor responsible for nest loss*			
		Predation	Desertion	Flood	Trampling
Laying stage					
1992	12	1 (8.3)	5 (41.7)	0 (0.0)	6 (50.0)
1993	13	5 (38.5)	7 (53.8)	0 (0.0)	1 (7.7)
1994	16	4 (25.0)	4 (25.0)	8 (50.0)	0 (0.0)
Total	41	10 (24.4)	16 (39.0)	8 (19.5)	7 (17.1)
Incubation stage					
1992	7	6 (85.7)	0 (0.0)	0 (0.0)	1 (14.3)
1993	9	8 (88.9)	1 (11.1)	0 (0.0)	0 (0.0)
1994	5	5 (100)	0 (0.0)	0 (0.0)	0 (0.0)
Total	21	19 (90.4)	1 (4.8)	0 (0.0)	1 (4.8)

* Numbers in brackets represent percentages of total loss due to factors for each stage.

prominent identified predators included the Jackal (*Canis aureus* Linné, 1758) and Banded Mongoose (*Mungos mungo* Gmelin, 1788), accounting for 50 % (n = 14) of the nests lost due to predation for the three years. The Red Monkey (*Erythrocebus patas* Schreber, 1775) accounted for about 20 % (n = 6) of the nests lost due to predation for the three breeding seasons. Other predators included monitor lizards (*Varanus sp.*) and snakes.

RE-NESTING

Out of the 62 birds that lost their nest during the study, 21 (33.9 %) re-nested (Table III). Of these, 5 were successful in their breeding effort which represents 19.2 % of the successful breeders (N = 26) for the three breeding years. In 1992, 28.6 % of the re-nesters were successful while in 1994, 33.3 % succeeded. No re-nesting was observed in 1993.

In 19 re-nesting cases (90.5 %), the re-nesting took place when the nest was lost during the laying stage. Only 2 (9.5 %) re-nested after incubation had started, but this was during the early stage of incubation. In one of the nests (belonging to a radio-tagged bird), re-nesting was not observed when the nest was trampled upon by elephants after 8 days of incubation.

NEST SURVIVAL

The daily nest survival rate varied from year to year, with daily survival during both the laying and incubation stages being lowest during the 1993 breeding season. Incubation lasted for 17 ± 2.0 days (± S.E., N = 26 nests) for all three years. Nest survival during the incubation stage was lower than during the

TABLE III

Re-nesting and re-nesting success for first-time and experienced breeding guineafowl hens.

Year	Re-nesters (N)	First-time breeders		Older breeders		Successful (% of N)
		re-nesters	successful	re-nesters	successful	
1992	7	5	1	2	1	2 (28.6)
1993	5	4	0	1	0	0 (0.0)
1994	9	6	2	3	1	3 (33.3)
Total	21	15	3	6	2	5 (19.2)

laying stage in 1992 and 1993, (Table IV). Nest survival during the incubation stage was lowest during the 1993 breeding season and highest during the 1994 breeding season.

TABLE IV

Guineafowl nest survival rates for the laying and incubation stages from 1992 to 1994.

Year	Total number of nests under observation	Nest days	Nests lost*	Survival per nest day ± 95 % confidence limits	Nest survival for the stage ± 95 % confidence limits
Laying stage					
1992	27	294	12 (63)	0.961 ± 0.0231	0.571 ± 0.1648
1993	26	273	13 (59)	0.955 ± 0.0258	0.521 ± 0.1660
1994	35	378	16 (76)	0.959 ± 0.0207	0.560 ± 0.1473
Incubation stage					
1992	15	138	7 (37)	0.949 ± 0.0374	0.508 ± 0.2067
1993	13	102	9 (41)	0.912 ± 0.0561	0.301 ± 0.1693
1994	19	198	5 (24)	0.975 ± 0.0223	0.717 ± 0.1863
Nestling stage					
1992	8	12	0	1.0	1.0
1993	4	6	0	1.0	1.0
1994	14	21	0	1.0	1.0
Whole breeding season (recruitment)					
1992					0.290 ± 0.0341
1993					0.156 ± 0.0281
1994					0.402 ± 0.0274

* Numbers in brackets represent the percentage of egg loss compared to the total loss for the whole breeding season (laying plus incubation stages) for each year.

The nestling stage lasted for only 1 ± 0.5 days ($N = 24$ nests). In one intensively followed nest, the bird left the nest about 6 hours after hatching was completed.

However, most of the birds stayed one or more nights with their flightless keets in their nest. Some birds (6) did not stay more than 2 nights in their nest after the nestling stage. Since no chicks were lost during the nestling stage in any year, this resulted in a survival of 1 for the nestling stage. Because the product of the probability of nest survival during the laying, incubation and the nestling stages gives the overall survival from the beginning of laying to the fledging of young (Mayfield, 1975), survival up to fledging of young (recruitment) was the same as survival up to the end of incubation. This recruitment (plus or minus the 95 % confidence limit) was 0.290 ± 0.034 in 1992, 0.157 ± 0.028 in 1993 and 0.402 ± 0.027 in 1994.

The hatching rate (the probability that eggs present at hatching time actually produce living young) for 1992 was 0.924 ($N = 8$ nests), in other words, 92.4 % of the eggs in the nest just before hatching started finally hatched into chicks. In 1993, the hatching success was 91.0 % ($N = 4$ nests) and in 1994 it was 95.0 % ($N = 14$ nests).

INFLUENCE OF FOOD AVAILABILITY

During all three years, there was a drop in the availability of both insects and seeds from the start of the first rains in March till June (Fig. 1). After this period, insects rapidly increased to their maximum number in July. Breeding each year started about a month (August) after the insect number has reached its peak. Seed density continues to decrease in number till August, after which it rapidly increases to a maximum by October when most eggs were already hatched.

INFLUENCE OF RAINFALL

The rainy season started later in 1994 (April) than in 1992 and 1993 (March), but 1994 received 841 mm of rainfall compared to 689 mm and 609 mm for 1992 and 1993 respectively. This rainfall figure was the highest recorded in the region over the last 10 years. There was a significant positive correlation between the annual rainfall and the breeding success which is equivalent to recruitment ($R = 0.98$, $R^2 = 96$ %, $P < 0.05$). A fitted regression of breeding success on rainfall was of the form $Y = -0.45 + 0.001\ X$, with t-values of -2.99 for the constant (-0.45) and 4.92 for the coefficient of X (0.001).

DISCUSSION

This study has shown that there is a statistically significant positive correlation between annual rainfall in the Waza region and breeding success in the Helmeted Guineafowl. Consequently, pairing starts in the Waza region between the months of March and April each year, which coincides with the start of the rainy season. Ayeni (1980) also reported that pairing started with the start of the rainy season between May and June in Nigeria in this species. Benson (1963)

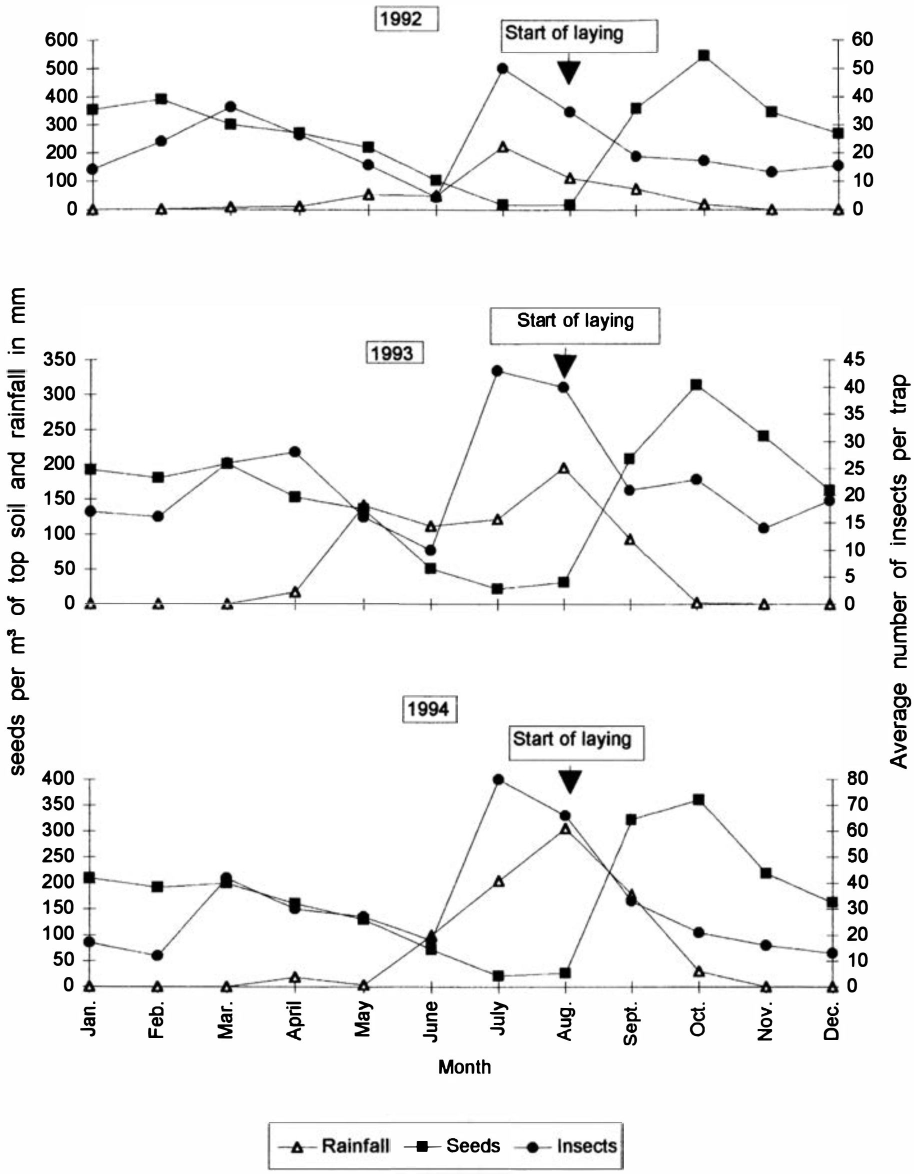

Figure 1. - Start of egg laying in the guineafowl in relation to monthly variation of insect and seed density in the study area.

suggested that the marked peak breeding during the rainy season in the Guineafowl might be linked to the abundance of insect food during this period. Fergin (1964) had suggested from studies of *N. meleagris* in Uganda that rainfall may directly or indirectly control breeding activities in this species. Crowe & Siegfried (1978) also found a high statistically significant correlation between the number of rainy days and the shooting index (index of guineafowl population density). Other studies have also shown that rainfall might influence breeding success in birds (Martin 1995).

In the Waza region, egg laying started in August for all three research years and continued till October. Maximum egg production coincided with the peak of the rainy season in August. The start of egg laying in this study (August) is later than was reported in neighbouring Nigeria (June) for the same species by Ayeni (1980). Crowe (1978) had also observed that rainfall might only be controlling the Guineafowl population in South Africa indirectly through the availability of protein-rich arthropods.

The annual mean clutch size in Waza (between 7.9 to 10.2 eggs for all nest found and 11.6 to 13.1 eggs for successful nests) is low when compared to 15 to 20 eggs reported for this species in neighbouring Nigeria by Ayeni (1983). The clutch size, however, falls within the 6 to 19 eggs reported by Clancey (1967) and McLachlan & Liversidge (1972). There has also been reports of an average clutch size of 80 to 100 eggs in the wild (Wyeld, 1977 cited in Ayorinde, 1987).

Re-nesting plays an important role in the Guineafowl's breeding strategy in the Waza area. In general, quantitative information on re-nesting is scarce (Beintema & Müskens, 1987). Up to 100 % re-nesting appears to be possible if nests were lost within the first week of breeding in some European meadow birds but it was noted that later in the breeding season, re-nesting became difficult (Beintema & Müskens, 1987). Re-nesting was also only observed in this study during the laying and early incubation stages. The absence of re-nesting when nest are lost in the late stage of incubation or just after hatching had also been reported in the Red Grouse (*Lagopus lagopus scoticus* Lath.) by Watson (1970) who suggested that re-nesting was controlled by a « psychological-endocrine » mechanism which became irreversible after hatching had taken place.

The observed incubation period of between 15 and 19 days is close to that of the Crowned Guineafowl (24 to 25 days) in South Africa (Farkas, 1965). Ayeni (1980) found that incubation took up to 27 days in *N. m. galeata* in Nigeria. Most probably, the incubation stage in his study might have included part of the laying stage that is considered as a different stage in the Mayfield's method the merits of which are discussed in Johnson (1979). However the duration of incubation can vary from year to year within the same species (Jenkins *et al.,* 1967 ; Jenkins & Watson, 1967) and also with clutch size (Jenkins *et al.,* 1963). So the longer incubation period reported in Nigeria might just been due to any of these conditions.

The hatching rates for the three years of this study (92 % in 1992, 91 % in 1993 and 95 % in 1994) are high when compared to those reported in Nigeria (between 28 and 34 %) by Ayeni (1980). His results, however, were from laboratory raised and from locally acquired semi-wild birds which might explain the low hatching rate since an uneven sex ratio, competitions amongst males and overcrowding in the laboratory might lead to some hens not copulating before laying eggs, with a resultant increase in infertile eggs. Ayeni (1980) also suggested that nutritional deficiency could be one of the causes of the low hatching rate in the Guineafowl he studied.

Low guineafowl population and poor breeding were reported by Skead (1962) and Mentis *et al.* (1975) during years with relatively low rainfall. Also, Mentis *et al.* (1975) and Crowe (1978) suggested that poor breeding success might be more a result of the influence of rainfall on the availability of high-protein insect food for the breeding birds rather than rainfall proper. It might also be possible that heavy rains reduce the proportion of nests lost to predators indirectly through the concealing of nests by good vegetation cover. In line with this, it was observed that the absence of good cover during the 1993 breeding season (the year with the highest number of nests lost to predation), led to some nests being located on bare ground, becoming more vulnerable. Although no nest loss was attributed to egg collection by man, it is widely believed by the park officials that hundreds of eggs are lost each year through this. In fact park records show that a good number of egg poachers had been arrested in the past.

First-time breeders produced fewer eggs and consequently fewer young than experienced breeders, which is consistent with most recent bird studies discussed in Martin (1995). However, Parcs (1963) and Szabo & Bankay (1974) observed that egg production in guineafowl hens could drop by as much as 20 to 30 percent after the first laying season which does not tie in with my results. This difference is not understood.

The peak of insect availability (July) occurs just before the start of egg laying in August. Seeds density was lowest during this period because most seeds had germinated. It is possible that seed food availability does not play an important role in the breeding of this guineafowl population since seeds were generally low in density during the breeding period, as can be seen in Figure 1. However, seeds becoming abundant after the birds have hatched may provide an additional source of food, especially as insect numbers start dropping after hatching is ended. Insect food availability on the other hand must be playing an important role in the breeding of this guineafowl population since the start of the breeding season always coincides with the period following high insect abundance.

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SUMMARY

The breeding success of wild Helmeted Guineafowl (*Numida meleagris galeata* Pallas 1767) was investigated for three consecutive years, from 1992 to

1994. The results show that egg laying starts in August. The breeding season usually lasted for about two months. Average clutch size for successful nests over 3 years was between 11.6 and 13.1 eggs. Nest abandonment, predation, trampling by elephants and flood were found to be the main causes of nest loss. The intensity of these factors varied with breeding stage and year. However, re-nesting compensated for most of the lost nests if the losses took place during the laying or early incubation stage. The age of the breeding hens also influences breeding success with older birds being more successful than first-time breeders. Nest survival was found to vary with breeding stage and rainfall, being highest (for all stages) in the year with the highest annual rainfall (1994) and lowest in the year with the lowest annual rainfall (1993). The overall breeding success plus or minus 95 % confidence limit was 29.0 ± 0.03 % in 1992, 15.6 ± 0.03 % in 1993 and 40.2 ± 0.03 % in 1994. The breeding season each year started about a month after insect number had reached its yearly peak.

RÉSUMÉ

La réussite de la reproduction de la Pintade commune sauvage (*Numida meleagris galeata* Pallas 1767) a été étudiée pendant trois années consécutives, de 1992 à 1994. Les résultats révèlent que la ponte débute en août. La durée de la saison de reproduction est de deux mois. Le nombre moyen d'oeufs par nid pour une excellente couvée est compris entre 11.6 et 13.1. L'abandon des nids, la prédation, le piétinement par les éléphants et les inondations se sont avérés être les causes principales de perte des nids. L'intensité de ces facteurs est fonction du stade de la reproduction et de l'année. Toutefois, une ponte de remplacement compense la majeure partie des œufs perdus si les pertes subies ont eu lieu au cours de la ponte ou du début de l'incubation. L'âge des femelles reproductrices influence aussi la réussite de la reproduction : les vieilles femelles sont plus aptes que les jeunes se reproduisant pour la première fois. La survie des oeufs d'un nid varie avec le stade de la reproduction et la pluviométrie : elle est la plus élevée à tous les stades en année de pluviométrie élevée (1994) et la plus faible en année de faible pluviométrie (1993). La réussite totale de la reproduction au seuil de 95 % de limite de confiance fut de 29 ± 0.03 % en 1992, 15.6 ± 0.03 % en 1993 et 40.2 ± 0.03 % en 1994. La saison de reproduction commençait chaque année environ un mois après que le nombre d'insectes ait atteint le maximum annuel.

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