[*From the* JOURNAL OF THE BOMBAY NATURAL HIST. SOC., *December 1957.*]

THE BLACKFACED WEAVER BIRD OR DIOCH IN WEST AFRICA:

AN ECOLOGICAL STUDY

BY

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(*With four plates, one text figure, and three graphs*)

During the last few years there has been growing concern at the damage done by the various subspecies of *Quelea quelea* to the grain crops in African territories. In some parts of the big thorn-scrub and savannah belt which extends from Sénégal to the Sudan and thence to Kenya, Tanganyika, the Rhodesias, and South Africa this bird has become a large-scale pest. Losses of wheat amounting to over two-thirds of the total crop have been reported in parts of East Africa, and similar damage has been caused to rice in Sénégal and sorghum in South Africa. No wonder this dioch is now compared by modern agriculturists to locusts in the losses which it causes!

The problem has even become so urgent that the governments of French West Africa, the Union of South Africa, and Tanganyika have appointed full-time zoologists to study the biology of the species in all its aspects, while other officers have been concerned with research into methods of control. To strengthen international co-operation in that field the Scientific Council of the Committee for Technical Co-operation South of the Sahara (C.S.A.) organised a first specialist conference on *Quelea* which was held in Dakar and Richard-Toll from 31 October to 5 November 1955. The proceedings of this important meeting have not yet been published in full, but a summary of the discussions has appeared in *The Ibis*, volume 98, 1956, pp. 538-541. A second specialist meeting on the same subject will be held this year in Livingstone, from 29 to 31 July, after the first Pan-African Ornithological Congress.

The French research programme on the ecology of the Blackfaced Dioch has been made possible through the generosity of the *Mission*

d'Aménagement du Sénégal (Sénégal Planning Council), a state organism mainly concerned with the agricultural development of the lower Sénégal Valley. A research station has been organised by the two junior authors (G.M. and M-Y.M.) at Richard-Toll, in the heart of the big irrigation zone which is progressively turning that formerly barren part of the country into rice-fields. Laboratory work and breeding experiments have been conducted there since 1953, when most field observations were made in the area shown in the accompanying map (figure 1). The senior author (F.B.) has been responsible for

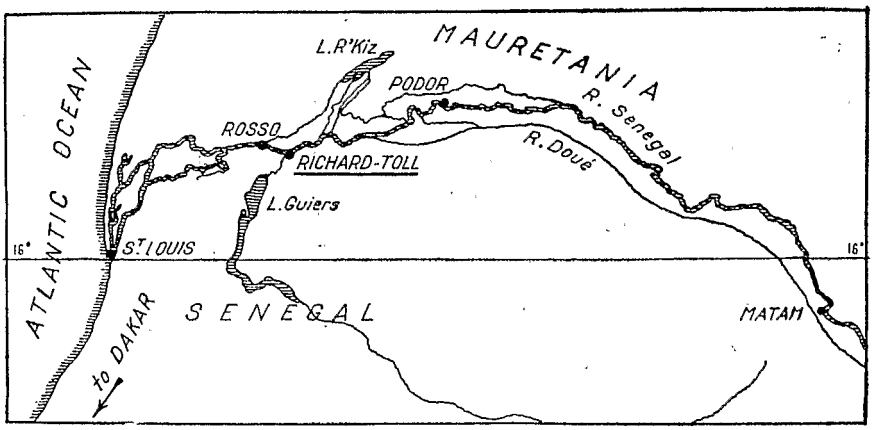


Figure 1. — Our study area, the lower Sénégal Valley.

the planning of the research programme and was fortunate enough to take part in two field trips, in April 1954 and August 1955.

The Bird

Three different subspecies of the Blackfaced Dioch are usually recognized. *Quelea quelea quelea* ranges from Sénégal to Bornu across the thorn-bush and grass savannah north of the Congo forest. *Quelea quelea aethiopica* lives in the Sudan and East Africa, intergrading in South Tanganyika and Northern Rhodesia with the South African subspecies *Quelea quelea lathami*.

The plumage of the typical race, to which our birds belong, show interesting variations. Normal males during the breeding season are usually easily recognized by their black face, their strong bright red bill, and the yellow edges to their primaries. The legs are salmon coloured and the eyes lined by a red eye-ring. But some specimens are quite different. The black forehead may be greatly reduced and even disappear completely. Moreover, the crown, the nape, the breast, and even the whole underside may be more or less suffused with pink. Such birds have been formerly given a special name (*Quelea russi*) but they merely constitute a phase—whose genetic mechanism still remains to be worked out—which can be met with in various proportions in the different populations. In our area it forms from 20 to 25 per cent of the male breeding population. The behaviour of such

birds does not appear to differ from that of the normal ones. The prenuptial moult starts at the very end of April and is completed in the middle of July.

In the middle of November, the males resume very quickly a sparrowy plumage; their beak becomes somewhat paler and they are no longer distinguishable in the field from the females. Such postnuptial moult appears to be rather strictly timed and sometimes abruptly interrupts a late breeding season.

Females keep a sparrow-like plumage all the year round, but show marked seasonal variations in the colour of the bill. During the breeding season it becomes lemon-yellow, turning red again as soon as the reproductive period is over.

Immature birds have the same sparrowy plumage as the females and the non-breeding males. When they leave the nest the bill is flesh-coloured and it does not turn red before the next breeding season. The postjuvenal moult does not begin before the end of January.

The Environment

The Blackfaced Dioch is a typical bird of the semi-arid (Sahelo-Sudanese) zone of West Africa.

In that part of the continent, the year is rather sharply divided into two periods of unequal duration: a long dry season from November to June, and a short rainy season from July to October. At Richard-Toll the average annual rainfall is of 350 mm., but important variations may occur from year to year, as shown in the following table:

Table 1

Monthly variations of the rainfall at Richard-Toll, from 1953 to 1956 (in mm.).

	1953	1954	1955	1956
May ...	0	0·6	2·8	0
June ...	29·5	18	52·5	0
July ...	58	25	90	29
August ...	121	182·5	143·8	42·2
September ...	130·2	22·5	87·8	212
October ...	56·2	5·7	15·4	36·7
Total ...	394·9	254·3	392·3	319·9

The rains bring on a spectacular change in the plant and animal life of this part of Africa. In a few weeks the parched thorn-bush turns into a pleasant park-like savannah. Insects become very numerous, flowers may be seen everywhere and many birds assume their breeding plumage.

The flora of our study area is not very rich, as compared with the southern parts of Sénégal and Gambia. The more numerous trees are two species of Mimosoideae, *Acacia senegal* and *Acacia tortilis*, and one Simaroubaceae, *Balanites aegyptiaca*. These are the

species regularly chosen by the Blackfaced Dioch to build its nests, and it seems worth noticing that all these trees are very thorny. Such is also the case with a bush of the genus *Zizyphus* which can also be used as support for the nests. On the contrary three other species of trees living in the same plant community, but without thorns, *Bauhinia reticulata*, *Bauhinia rufescens* (Caesalpinioideae) and *Leptadenia spartium* (Asclepiadaceae) are never used by *Quelea*. On seasonally flooded areas, along the Sénégal River, dense stands of *Acacia scorpioides* are found. They are seldom used by *Quelea*.

The grassy stratum is made up principally of a number of species of Gramineae whose seeds constitute the staple food of the adult Blackfaced Diochs all the year around. Millet (*Sorghum* and *Pennisetum*) grown near the human settlements, and rice now introduced in the irrigation zone around Richard-Toll, are to be added, of course, to the list of the seeds regularly eaten by these birds. The amount of grain actually consumed by the diochs is nevertheless but a small part of their depredations, far more rice being crushed and spoilt by the weight of the birds alighting on the crop than eaten by them!

Life History

The Blackfaced Dioch is an extremely gregarious bird, living in flocks all the year round. During the rainy season adults usually gather in large colonies harbouring millions of birds. Once the breeding is over these huge swarms break up into much smaller flocks which scatter over the whole semi-arid belt. Such flocks nevertheless usually congregate for the night in densely packed roosts, very often located in the same places from year to year. Both nesting colonies and nocturnal roosts of the non-breeding season thus offer excellent targets for control of the birds, and have so far proved most vulnerable.

Our description of the life-history of *Quelea quelea*, as summarized in the present paper, is based on studies made both in the field and in captivity. From 1953 to 1956 we were able to study closely numerous nesting colonies located in various parts of the lower Sénégal Valley. Such field-work enabled us to describe the various stages of nest construction, and to make extensive observations on clutch-size, growth, food-consumption, and mortality of the nestlings. Moreover, we were lucky enough, in 1955 and 1956, to breed for the first time Blackfaced Diochs in captivity, in our aviaries at Richard-Toll. Thus we were able to analyse more closely the various behaviour patterns of this gregarious weaver and to make preliminary experiments on the influence of some ecological factors which probably play a role in the timing of their reproductive cycle.

Nesting Sites. In our area nesting always takes place in thorny trees, mainly *Acacia senegal*, *Acacia tortilis* and *Balanites aegyptiaca*, and is always colonial. A certain density of trees is therefore necessary for the establishment of the big colonies and we have so far found an average of 50 trees per hectare[1] to be the rule

[1] 1 hectare = 2·471 acres

in most cases. But in some nesting sites the density of trees can be much higher, up to 300 per hectare.

The number of nests per tree is even more variable, from a few scores to more than a thousand. On the average a five metre high acacia tree harbours about 200 nests, but the *Balanites*, probably on account of their countless long spines, may be covered by thousands of nests and look like hay-stacks.

The size of the nesting colonies is likewise variable. Fifty hectares can be taken as an average, but colonies as large as 400 hectares have been found. The total population of such aggregations is therefore tremendous. If we take, for instance, an average colony of 50 hectares where the number of trees is 50 per hectare and the number of nests 200 per tree, we reach a rough total of 500,000 nests! This is an average figure and the largest colonies can certainly contain up to 10 million nests.

Some very small nesting colonies are nevertheless met with from time to time. In 1953 we found near Dara (100 km. north-east of Rosso) in Mauretania very small colonies established in scanty gum trees between sand dunes. Again in 1954 we found colonies of less than 10 trees, and H. J. de S. Disney and J. W. Haylock (1956) tell us of similar small nesting sites in the Rift Valley. On the other hand, our breeding experiments of 1955-1956 conclusively establish that a colony of as few as five pairs of Blackfaced Dioch can reproduce successfully.

Besides a sufficient density of trees, the establishment of a nesting colony of *Quelea quelea* seems to require at least two other environmental conditions: the vicinity of water and sufficient herbaceous cover. As a matter of fact the nesting colonies are never located very far from rivers, lakes or at least temporary water holes, and that explains probably why the nesting sites are so numerous around R'Kiz Lake and along the banks of the Sénégal River. Moreover, the quantity of grass necessary to build so many nests and the amount of seeds needed to support millions of birds during the whole breeding season make the presence of a dense cover of Gramineae an absolute necessity.

The combination of these various requirements—a sufficient density of trees, the proximity of water and the presence of a dense grass cover—probably explains why Blackfaced Diochs show some tendency to use again their old nesting sites, despite their regular destruction. This is quite obvious around R'Kiz Lake in 1954, 1955, and 1956, and similar instances have been reported in Tanganyika.

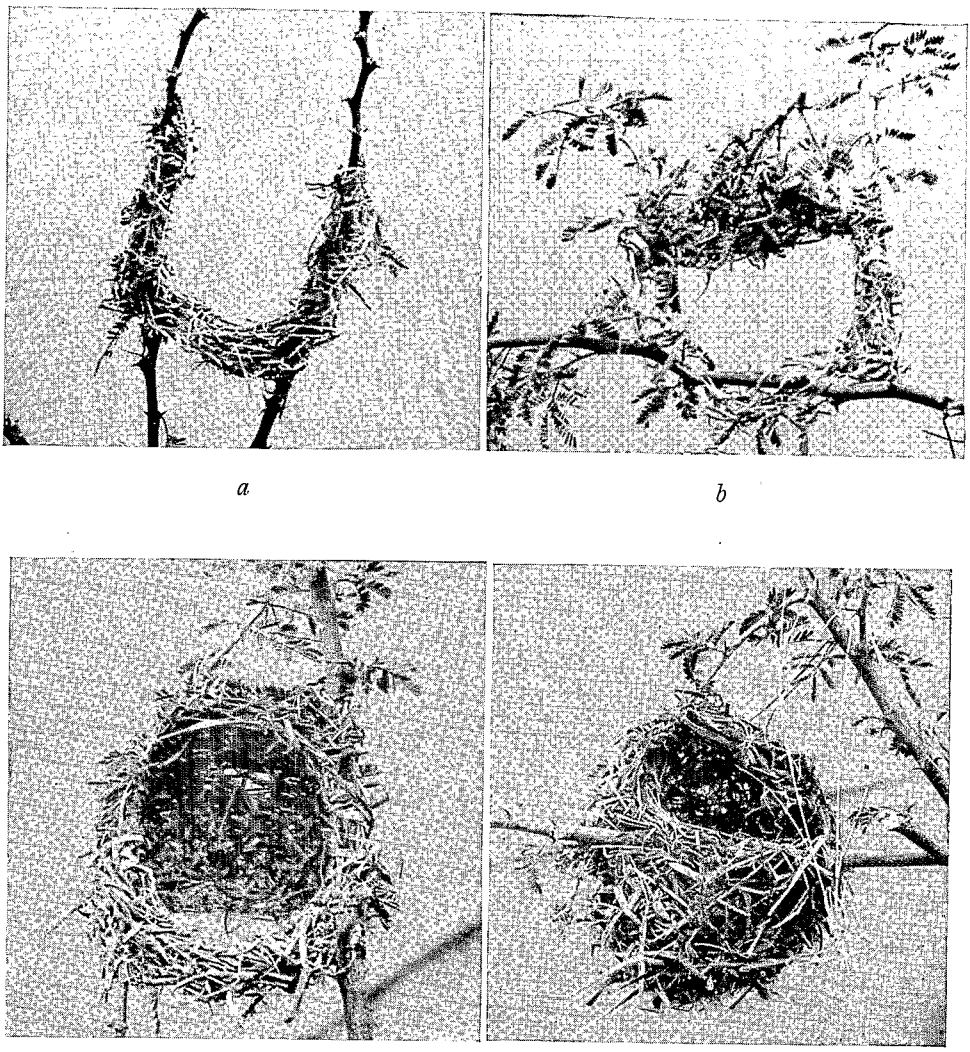
In some places *Quelea quelea* breed in rushes over water, despite the presence of apparently suitable trees in the neighbourhood. Such is the case in some parts of the French Sudan (Dekeyser, 1955) and also in East Africa. As yet, we have not found any evidence of the presence of this 'juncicole type' in our study area.

Nest-building and Pair-formation. *Quelea*'s nests are rather loose but strong round structures, firmly attached to the surrounding twigs and thorns. They do not hang nor do they have a funnel-like entrance like so many weavers' nests, and are made entirely of grass.

They are built by the males which start by twisting and knotting, mainly with the bill, long green stems of Gramineae around surrounding twigs or thorns; such a 'bridge' is then rapidly enlarged into a crescent-like structure which gradually becomes an upright ring. Work proceeds by the construction of the roof and the sides of the nest (double opening stage) before completing the cup (pocket stage).

These first stages of the nest building do not take a long time—about four days according to our field observations at El Khatt colony in August 1955. At that time the males are often seen displaying in a very peculiar manner. They raise and flutter their wings, elevate their tail, fluff slightly their contour and head feathers and sing a short sentence. Such a posture has been called 'butterfly display' by J. H. Crook (in preparation) and 'territorial display' by Morel and Morel (1957). The function of such a display is obviously to attract the females which are starting to visit the constructing males at that time. During our 1956 breeding experiments one of our males regularly indulged in butterfly display when a female was nearby. But this posture may likewise be assumed to threaten a male intruder, as shown by our observations at the Palm Grove colony on August 24, 1955, and in our aviaries on October 21, 1956, when two marked males were trying to build together the same nest. The aggressiveness of the males during these first stages of the nest building is very strong indeed, and their territorial behaviour well developed. Actual fights are frequent and death of one of the antagonists may ensue. Under a single small tree, on August 25, 1955, at the Hassi Leben colony, we found the dead bodies of two males, one with the right eye torn out. That is why we misinterpreted at first this posture and called it 'intimidation display' (Morel and Bourlière, 1956). The butterfly (territorial) display is seen during the first four stages of the nest-building, until the pocket stage. When a male has abandoned a first nest and started building a new one, it resumes that posture.

At about the fifth day of nest-building, when the whole structure is almost completed but the entrance still too large and lacking the 'pent house', the male stops building and pair-formation takes place. As early as the 'pocket stage' males get more and more interested in the visiting females and butterfly ('territorial') display gives way to the 'connubial display'. Both sexes quiver more or less quickly their half spread and dropped wings, fanning their tail and fluffing their contour feathers. Initiative is usually taken by the male, but sometimes by the female. In 1955 we thought that the yellow bill of the mature female could act as the specific releaser of pair formation in *Quelea*, and we accordingly undertook a few field experiments with dummies (stuffed females with bills painted yellow or red). Our observations failed to disclose any obvious difference between the response to the yellow-billed and the red-billed dummies; both were attacked by the male 'owners' when placed on their nests. On the other hand, a small proportion of females retain a pink bill at the time of pair formation; on August 24, 1955, at the Hassi Leben colony, we found that 60 out of 270 females (i.e. 22%) still had a more or less reddish bill. Both kinds nevertheless behaved in quite the same way.



a *b*

c *d*

The various stages of nest construction in *Quelea q. quelea*. *a*. The "crescent" stage, *b*. the "ring", *c*. the "double opening" stage, *d*. the "pocket" stage.

Photos : F. Bourlière

The connubial display near the still unfinished nest.

Photos: G. Morel

The duration of the pair-formation stage is quite short. At El Khatt, in August 1955, the first copulation was noted on the 24th at 10.40 a.m., but the same day at 6.15 p.m. we watched a 'frenzy of copulations' everywhere in the colony. The next day no more copulations were noticed and the first eggs were laid. As soon as the pair is formed it remains stable and the males pay no attention to the unattached females displaying near their nests. Both sexes take part in the defence of the nest, but we never observed the female adding material to it. The nest itself is quickly completed by the male, but no lining is added and the structure remains quite permeable. Neither eggs nor nestlings seem to suffer from such a situation, even after a prolonged night storm (Hassi Leben, 1954).

On the whole, the building of these colonies harbouring millions of birds does not take more than a week. Tons of green grass must therefore be readily available to afford the necessary material.

The bigger colonies of Blackfaced Diochs appear to exert a strong attraction on the smaller ones which happen to be present in the neighbourhood and which may be deserted at a more or less early stage. At the beginning of the breeding season of 1955, swarms of *Quelea* were watched from an observation plane by M. Bessac leaving their nesting places south of R'Kiz Lake and heading towards the Hassi Leben colony where they settled to breed. Such unsustained attempts at nesting have also been observed in 1954 and 1956; this behaviour deserves closer study.

In all breeding colonies so far studied the sex-ratio of the adult birds was found to approximate 50 : 50. No evidence of polygyny has ever been found.

Egg-laying, Incubation, and Development of the Young. The first eggs are laid 24 hours after pairing and before the nest is completed. As a matter of fact laying often takes place when the structure is still so thin that the eggs can be seen from outside. In some cases the urgency to lay causes females to drop their eggs on the ground. On August 25, in the morning, under a small tree of the El Khatt colony, we found no less than 20 such eggs!

Clutch size, as discussed later in this paper, ranges from 1 to 6 eggs, clutches of three being the more numerous. Larger clutches (35 eggs in one case) are certainly due to the laying of several females in the same nest (Lemoileh colony, 1954). Such abnormal clutches were spontaneously abandoned by the birds. *Quelea* eggs are 18.3 × 14.2 mm. in size and are a pale greenish blue in colour with no markings.

Brooding is carried out by both the male and the female by day, but at night only the female broods (Boul colony, 1953). In the daytime, incubating parents never stay for a long time on their eggs. On September 4, 1955, for instance, a female was seen to leave and enter her nest 21 times during 41 minutes of continuous observation. Such brief periods of actual sitting has been noted in every colony we have studied as well as in our aviaries. Such a peculiar brooding behaviour is probably made possible both by the very high environmental temperatures (which can reach 40° C. in the shade at noon)

and by the loose structure of the nest (which prevents overheating). That *Quelea* eggs do not need close attendance to be able to hatch is proved by an experiment we made in 1956 at the Hassi Leben colony. On October 6, eggs were collected at random from various nests and kept for two days under our tent before being subsequently replaced in occupied nests. On October 15, these 26 eggs which had not been brooded for almost 50 hours had given birth to nine apparently normal young.

During incubation the connubial display gives way to a slightly modified posture which we called 'greeting display' (Morel and Morel, 1947). Whenever a bird arrives on the nest, both male and female start quivering their half-spread wings which are held at an horizontal level (and not dropped as in the connubial display). Moreover, the contour feathers are held sleek and not at all fluffed out. Such behaviour has quite probably a social significance, helping to maintain the pair-bond.

Territorial behaviour and aggressiveness continue to be noted during the incubation period. As before, the territory continues to be restricted to the nest itself and its immediate surroundings, like the favourite perches close to its entrance. Both sexes take part in its defence as shown by our 1955 experiments with stuffed birds placed on the nests at various stages of the incubation period. Threat displays used in territorial defence can consist simply of facing the intruder and pointing the bill in its direction, until it flies away. Meanwhile the 'owner' fluffs its head and contour feathers, often raises and spreads its tail, utters a harsh sound, and often makes a few intention flight movements. When the intruder gives up, it lowers its head while the winner keeps its own raised. When such a threat does not suffice, the 'owner' may chase the intruder and actual fights take place. Robbing straws from the nest frequently releases such aggressive behaviour.

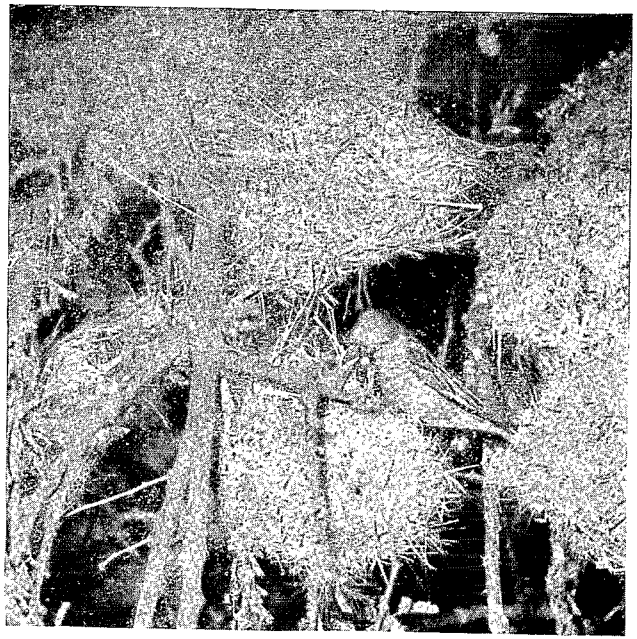
Both in the nesting colonies we studied in Mauritania in 1955-1956 and in our aviaries in 1956, the incubation period lasted 12 days.

The nestlings are fed by regurgitation from the parents' crop on a mixture of little grass seeds and insects, mainly grasshoppers and caterpillars. Hemiptera and Diptera can also be taken. The amount of insects eaten by the young Blackfaced Diochs for some days after hatching ranged from 35 to 50 per cent of the total volume of food found in the 433 crops collected in 1953 and 1954.

Both parents share the feeding of the young, as shown by the continuous observation of a nest at Boul's colony on October 16, 1953.

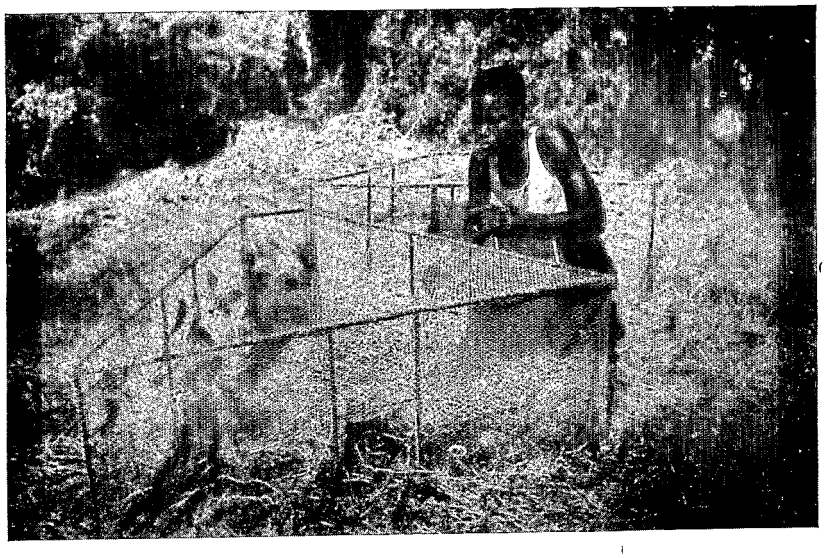
Adults do not forage alone to collect the food needed to raise their brood. As soon as they have delivered their crop content to their young, parents usually fly to the top of the nesting tree and wait till a foraging flock flies by. They join it immediately and thus go away from the colony. It is likely that such birds usually collect their food at short distances from their nesting place; but that is not always the case. At the Tambass colony, for instance, we found in 1954 rice seeds from the ricefields of Richard-Toll (25 km. away, as the crow flies) in the crops of some young.

Males "standing guard" on their nests. Incubation stage.

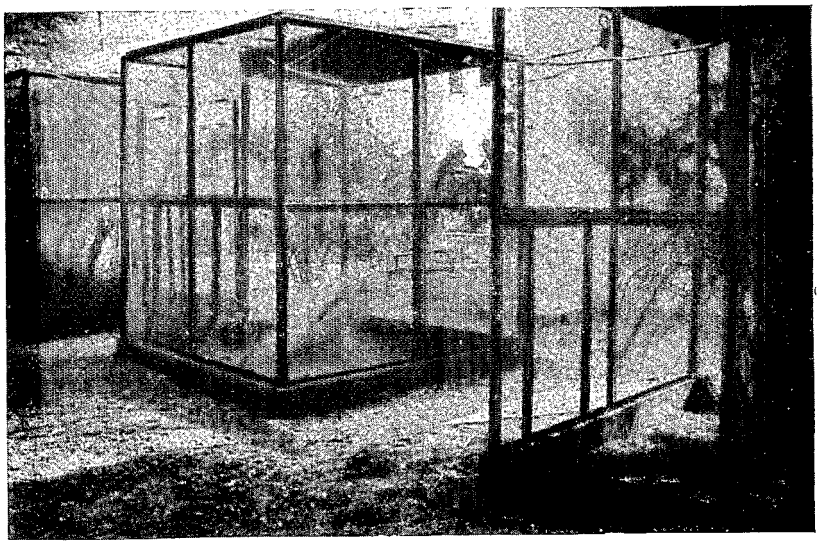


Male feeding the young.

Photos: G. Morel



The traps used for catching immature Queleas.



The aviaries for breeding experiments, Richard-Toll Ornithological Station.

Photos : G. Morel

Territorial behaviour seems to become less conspicuous soon after hatching, as shown by our 1955 dummy experiments. Aggressiveness still persists against intruders, but both parents are so busy gathering food that they have little occasion to spend much time near their nests. Nest-sanitation has been noted only during the week following hatching. Later on droppings are no longer removed and accumulate in the bottom of the nest.

The young were first observed to leave the nest on their 14th day, both in the nesting colonies and in our aviaries. By that time their food consists almost entirely of grass seeds, which they still beg from their parents for at least five days. In the meantime they start foraging on their own, dropping down to the ground underneath the trees and picking up seeds, and even eggshell according to Disney and Haylock's observations made in Tanganyika. In November 1956, fledgelings had not yet left the Hassi Leben colony 19 days after hatching (J. H. Crook, personal communication). When they have abandoned their nest, the juveniles continue to roost for a few days beside it. Later they concentrate together at night, and finally leave the nesting site to roost elsewhere some five days after climbing out of the nests.

Females are ready to breed at the age of one year. Two of our marked birds (white and violet) hatched in our aviaries on September 5, 1955, successfully paired and laid their first eggs in October 1956.

The sex-ratio of the young *Quelea quelea* appears to be almost equal, as shown by the following figures:

TABLE 2

Sex-ratio of the young

—	Age (days)	Total of young	Males	Females
Tambass colony, 1954 ...	1–2	525	279	246
Lemoileh colony, 1954 ...	1–3	313	159	154
Tambass colony, 1954 ...	8	182	86	96
Dara colony, 1953 ...	14	136	71	65

The average number of young raised is a little over two per nest—Tambass colony, 1954: 2.08 (266 nests); Hassi Leben colony, 1955: 2.7 (614 nests); Hassi Leben colony, 1956: 2.2 (436 nests).

Clutch replacement and Second Brood. On October 8, 1953, at Boul's colony, we removed the whole clutch in 8 nests which were at half their incubation period. No clutch replacement took place. However, it has been assumed that the late (and mostly unsuccessful) colonies, which are met with from time to time, could have been built by birds whose nests had been destroyed by the *Office de Lutte Antiaviaire* (Bird Control Service) earlier in the season. Such could have been the case, for instance, with the small colony established round the 20th of October 1956 near Ross-Bethio, half way between Richard-Toll and Saint-Louis; the season was so much

advanced that about two-thirds of the nests were abandoned shortly after laying or even after hatching. Until a large number of breeding birds are banded it will be impossible to be sure of that point.

The possibility of a second brood does nevertheless exist. During our 1956 aviary experiments, a marked pair (green male × white female) raised a first brood (4 eggs, 2 young) in nest 1 in October, and the one-year old female laid a second but unsuccessful clutch of 2 eggs in nest 3 (which had been taken up by her mate) on November 11.

The Adults outside of the Breeding Season. As soon as the nesting period is over, Blackfaced Diochs scatter all over the sunburnt savannahs in parties of at most several hundred birds. These small flocks spend most of their time on the ground, scratching it with their feet and bills, searching for the ripe grass seeds which have then fallen down. When frightened by some unusual noise or movement, they take off abruptly—producing a noise which can be heard at long range—and fly some distance before resuming their foraging.

At noon and during the hottest part of the day, the birds like to rest in thick cover to preen and chatter. The duration of such a midday rest appears to depend on the abundance of food. When it is scarce the diochs are busy feeding most of the day, but when it is plentiful and readily available they spend a lot of time resting in some shaded place. That is what happens, for instance, on the large ricefields near Richard-Toll when the crop is ripe. During December 1954, a huge diurnal roost was thus observed at harvest time in a small wood, at about one mile from the fields as the crow flies. Here the birds used to spend hours every day preening, chattering, bathing nearby, or weaving grass around twigs, or even building mock-nests not exceeding the ring stage.

Feeding activities come to an end late in the afternoon and the small flocks can then be observed everywhere, making for their communal night roost, gathering together in certain places before flying to the roost, where they usually arrive in the last half-hour of daylight.

The location of these huge roosts is about the same every year. They are usually located in acacia trees not very far from water, Blackfaced Diochs liking to drink before going to sleep. During the colder months (December to February) when the night temperature may fall to 15° C., they seem to prefer dense reed-beds which probably provide them better shelter. The birds usually leave the nocturnal roosts as the sun rises, the swarm breaking up into a few dense flocks which fly away in different directions before scattering in smaller parties.

Both male and female appear to spend the night in the same roosts, but an intriguing disproportion of the sex-ratio has been disclosed by our 1954 observations. During that year we examined 3,695 adults killed by blasting in 10 roosts along the Sénégal River. Out of these birds we found only 946 females, i.e. about three males to one female. H. J. de S. Disney and Haylock (1956) have also noted that, especially after nesting, flocks may consist almost entirely of males.

Anyway that is a very perplexing problem, as one considers that the sex-ratio among nestlings has always been found to be equal.

The huge bird-clouds on migration reported from East Africa have not been reliably observed in Sénégal or Mauretania up to the present time. Our ringing experiments seem to prove that the birds born in our area stay there and do not wander very far. Out of 970 immature birds banded in Richard-Toll between April and August 1954, 80 were recaptured later at the same place. One young banded early in April was nevertheless found near Dakar (at 250 km. SW. as the crow flies) early in July.

Flocks of juveniles do not seem to merge with adult parties immediately after the breeding season, and for some months the young of the year keep together. Such gatherings are very common around Richard-Toll during the last months of the year. Out of 5,520 birds banded at our station between November 13 and December 26, 1956, no more than 15 were adults.

About a fortnight before breeding the birds start gathering around their usual nesting place. That is the time where unsustained attempts at nesting are reported every year in Lake R'Kiz area.

QUELEA AND ITS ENVIRONMENT

The Blackfaced Dioch seems to be influenced in many ways by the fluctuations of some environmental conditions. Early in the course of this study, we were impressed by the fact that not only were the time and duration of the breeding season obviously related to the timing of the rains, but also that the productivity of the colonies was in some way adjusted to the carrying capacity of the environment. The quantitative study of these interrelations therefore became the main long-term objective of our field observations and of our experimental work. It will probably take us many more years to reach the stage where definite conclusions can be drawn, but some of our preliminary results seem nevertheless worth recording at the present time.

The Timing of the Breeding Season. The various ecological factors which control the breeding cycle of tropical passerines are still very poorly known. As the seasonal variations of the photoperiod are quite small close to the Equator, their influence on the reproductive cycle has been questioned by many ornithologists. On the other hand the effect of the rains cannot be underestimated. We have therefore tried to disentangle the respective influences of these various factors, both by experimentation and by field observations.

That the avian gonads are still able to respond to an artificial increase of daily illumination, at the latitude of Richard-Toll (16° 25′ N.), is shown by our 1955 experiments. From February 2 to June 12, 23 Blackfaced Diochs (11 males and 12 females) were given a daily supplement of light of five hours (from 7 to 12 p.m.). 17 other birds were kept as controls in another aviary and fed, like the experimental animals, on rice and millet. Such an artificial increase of the photoperiod was quickly followed by an increase of the gonads of both

sexes, an early appearance of the breeding plumage, and a premature moult of the remiges.

When 12 out of 13 controls had, on June 15, testes which did not exceed 3 mm. in length, 4 'treated' males had testes ranging between 10.5 and 5 mm. and 5 others ranged between 5 and 3 mm.

The black face of the males and yellow bill of the females appeared much earlier in birds which enjoyed a daily supplement of light than among controls. On April 27, for instance, three males had already a perfect black 'mask', when all the controls still kept their sparrowy plumage. On June 12, nine males had their full nuptial dress, as compared with a single control bird.

J. J. Marshall and H. J. de S. Disney have reported very similar results during their work on *Quelea quelea aethiopica*.

An artificial increase of the daily illumination seems, moreover, able to hasten the sexual maturity of young Blackfaced Diochs. On December 8, 1955, one of the young *Quelea* born in our aviaries on September 4, and provided since that time with a daily supplement of five hours of light, already had an half-grown black face!

All these preliminary experiments seem to indicate that the increase in the day-length which takes place from January to June plays a major role in regulating the seasonal enlargement of the gonads of Sénégal's *Quelea*, as it does in passerines nesting much farther north. Once the nuptial plumage is completed and the gonads have attained their full size, the birds are physiologically ready to breed. But actual nest-building does not start at once, nor does it take place at the same time every year. Some more 'proximate' factor must therefore regulate the beginning of the actual nesting season. The rains, in all probability, play this role, more or less directly. Blackfaced Diochs cannot start building their huge nesting colonies before the cover of grass is dense enough to provide them with the tons of material they need to build their millions of nests. Nor can they raise their broods before the insects are abundant enough to compose some 50 per cent of the diet of the young birds. Both the growth of the grass cover and the build-up of a sufficient insect population depend finally on the rains. Until the first showers fall the soil remains barren or covered with straw useless for weaving, and insects are scarce.

No wonder that the *Quelea* nesting season coincides so closely with the rains. Such a correlation becomes obvious when one compares the breeding seasons of the Blackfaced Dioch in West African areas whose rainfall pattern is different. In the upper valley of the Sénégal River (around Matam), for instance, where rains start generally one month earlier than in the Lake R'Kiz area and in the lower valley, nesting likewise begins earlier. In our area the time when actual nest-building takes place varies also from year to year and these variations follow those of the rains. During an average year, like 1953 or 1954, nest-building starts early in September. When the rainy season begins earlier, as in 1955, the birds likewise breed ahead of schedule (nest-building during the second half of August). On the contrary, when the rains are late, as in 1956, the breeding season is postponed and the birds do not start building their colonies till the very end of September.

We still do not know how that rain-stimulus works. We are nevertheless inclined to believe that it acts through its effect on vegetation. Indeed the Blackfaced Diochs never breed immediately after the first rains. On the contrary they seem to wait till new grass is sufficiently grown to enable them to build their nests and to provide them in due time with fresh seeds (and insects) to feed the young.

The Limiting Factors. The factors which control population size in tropical Passerines are still poorly elucidated, and *Quelea quelea* obviously offers an excellent opportunity for such a study.

Food. In years when the rains start very late in the season and are less abundant than usual, thus reducing the amount of food available, both clutch-size and nesting success are smaller than in years when the rainy season is longer and heavier. That was the case in 1956 as compared with 1955 (see tables 1, 3, and 4). The scarcity of broods of more than three fledgelings in such 'bad' years is

TABLE 3

Yearly variations in the clutch-size of *Quelea quelea*, Lower Sénégal Valley, 1953–56

Clutch size	1953	1954	1955	1956
1 egg ...	4 (3·1 %)	121 (5·8 %)	59 (4·1 %)	58 (5·9 %)
2 eggs ..	39 (30·7 %)	467 (22·5 %)	194 (13·5 %)	240 (24·6 %)
3 eggs ...	72 (55·9 %)	1228 (59·7 %)	819 (57·3 %)	475 (48·7 %)
4 eggs ...	12 (9·5 %)	230 (11·1 %)	319 (22·3 %)	188 (19.2 %)
5 eggs		18 (0·8 %)	37 (2·5 %)	14 (1·4 %)
Nests studied ...	127	2064	1428	975
Average clutch-size...	2·72	2·77	3·06	2·85

remarkable, and is quite probably explained by the increased nestling mortality in broods of larger size when the food is not abundant enough. In October 1956 we weighed nestlings at the Palm Grove colony, in nests containing respectively 2, 3 and 4 young. The result is shown in Figures 2 to 4. Not only were the young of larger broods found to weigh rather less when leaving the nest than those from smaller ones, but also the mortality rate in broods of 3 and 4 young was definitely greater than in broods of two. The death of the youngest and weakest nestlings was frequently observed. Furthermore, the fledgelings differed considerably in weight. In nest no. 65, for instance, the larger one weighed 15.9 g. when the smaller reached only 10.5 g. Now, the chances of survival of the fledgelings after leaving the nest are probably very much affected by their weight. Early in December 1956, we were visited in Richard-Toll by large flocks of young birds which had left their nests a few weeks before —some patches of down being still visible on their heads. Those juveniles were obviously starved. Not only was their weight lower than the average, but some were observed gathering around our aviaries and begging for food from our captive adults through the

wire-netting. Some were found dead around the station and many more (around 10%) died after being trapped for banding, although they were handled carefully and given food and water.

During the next breeding seasons we hope to be able to get quantitative data on the amount of vegetable and insect food available, together with the quantity actually consumed by parents and nestlings. The biomass of available insects will be estimated through the amount collected per night in traps using ultra-violet light.

TABLE 4

Yearly variations in nesting success

R'Kiz area colonies, 1955 and 1956

	1955	1956
Nests with 1 young ...	40 (6.5%)	60 (13.7%)
Nests with 2 young ...	200 (32.5%)	227 (52·0%)
Nests with 3 young ...	277 (45.1%)	146 (33·4%)
Nests with 4 young ...	82 (13.3%)	3 (0·6%)
Nests with 5 young ...	15 (2.4%)	——
Nests examined ...	614	436
Average number of young.	2.7	2.2

Predation. *Quelea*'s predators are rather numerous, but their pressure at the population level does not seem to be very great. During the breeding season we frequently observed Tawny Eagles (*Aquila rapax*) alighting on the nesting trees, tearing open the nests and eating the young. Marabou Storks (*Leptoptilos cruminiferus*) behave much in the same way. The Redbilled Hornbill (*Tockus erythrorhynchus*) is also fond of young Blackfaced Diochs; it easily picks up the nestlings through the nest entrance with its large curved bill. Pythons likewise prey upon the young *Quelea*, as does the Beaked Snake (*Rhamphiopis rostratus*) in East Africa.

Man has undoubtedly now become *Quelea quelea*'s main predator. With the development of modern methods of control (explosives, flame-throwers) millions of adults and nests are destroyed every year. If there is no large exchange of population between the Sénégal Valley and adjacent regions, the species should quickly decrease in numbers in our area.

Longevity in the Wild. Data on the maximum duration of life of the Blackfaced Dioch in captivity are unfortunately still lacking. On the other hand, we have started ringing our birds since too short a time to have any precise idea of their expectation of life in the wild. A few recoveries of birds banded when juveniles nevertheless give a first indication on their maximum longevity.

These preliminary results show that 1.3 per cent at least of the 970 juveniles born during the 1953 season and banded during 1954, still stayed in our study area four years later. Similarly, out of the 228 juveniles of the 1954 season banded in 1955, 2.6 per cent at least were

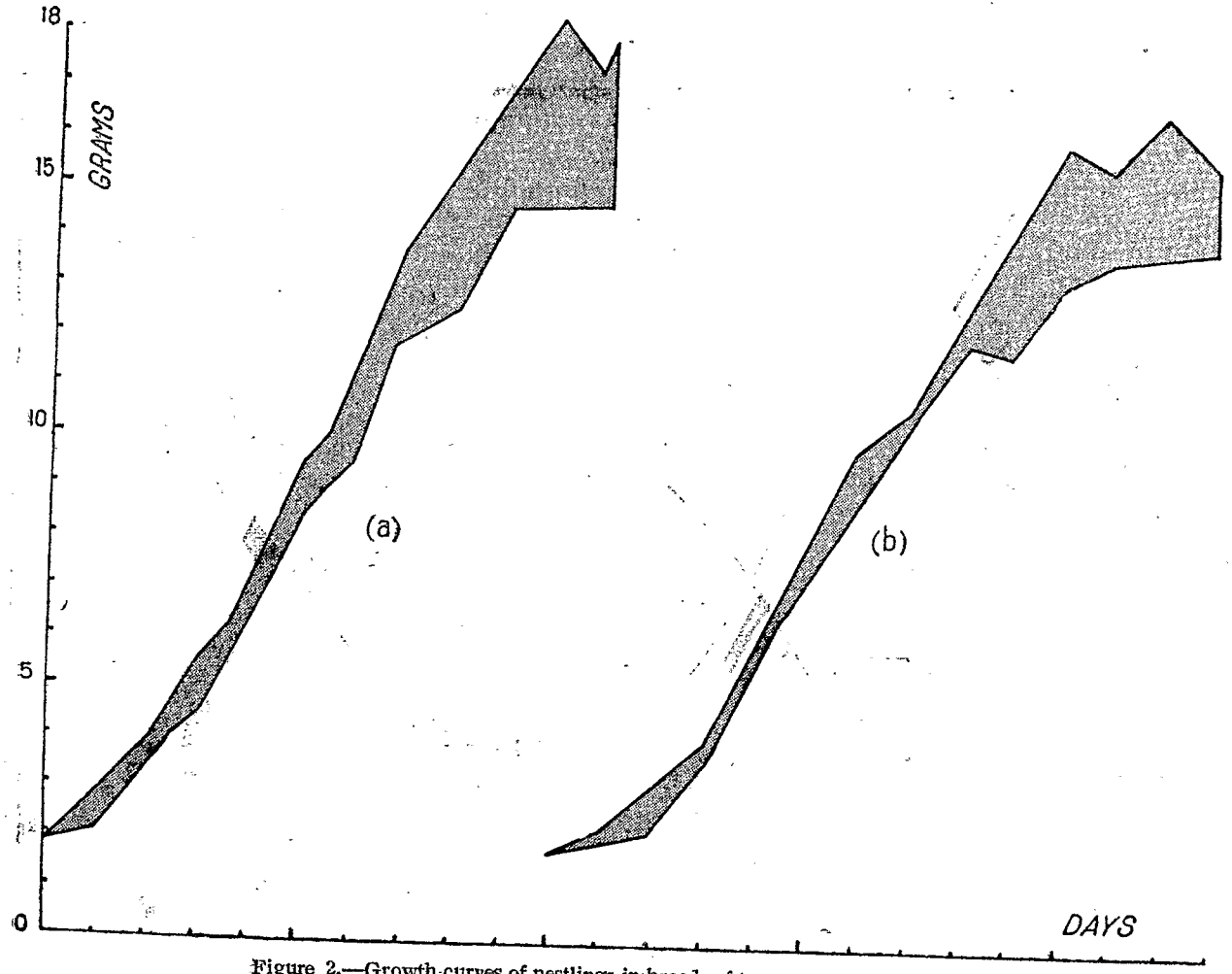


Figure 2.—Growth curves of nestlings in broods of two young, October 1956.

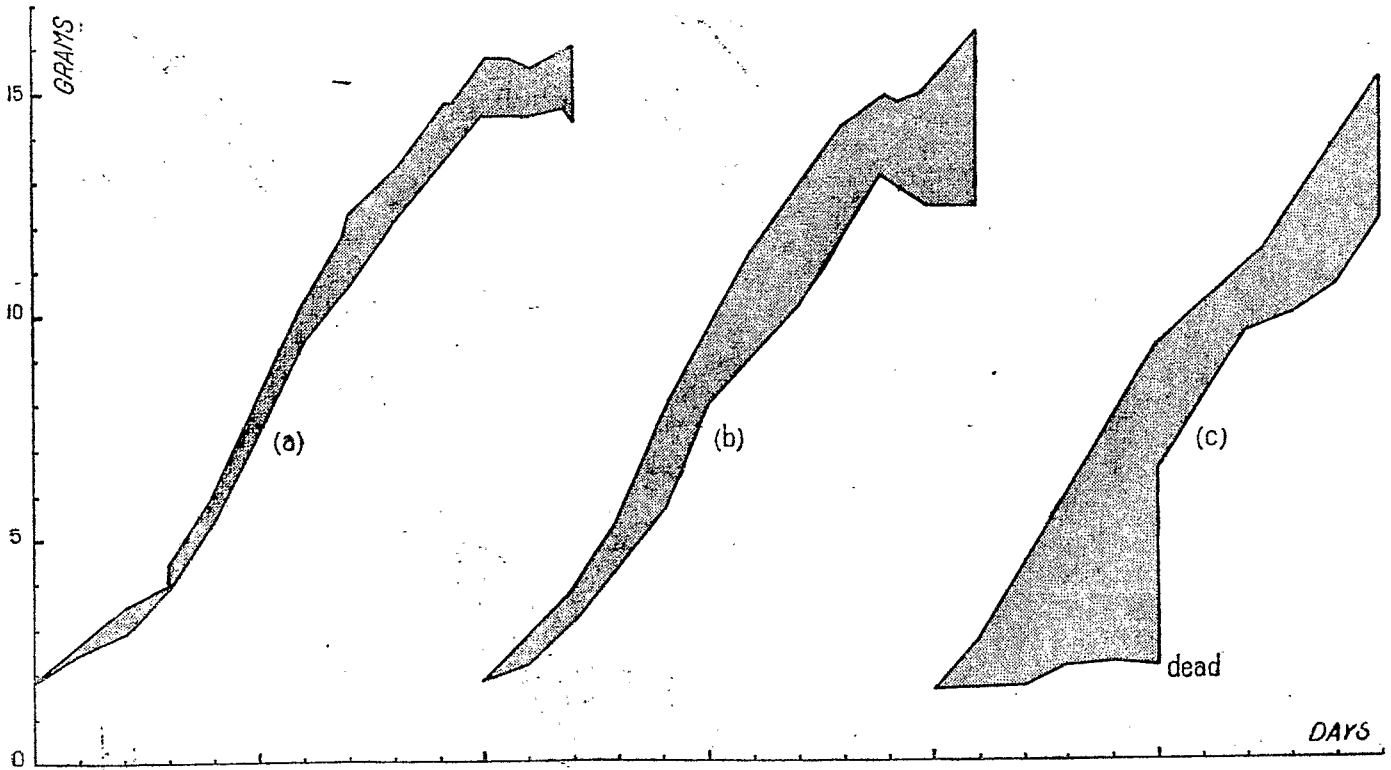


Figure 3.—Growth curves of nestlings in broods of three young, October 1956.

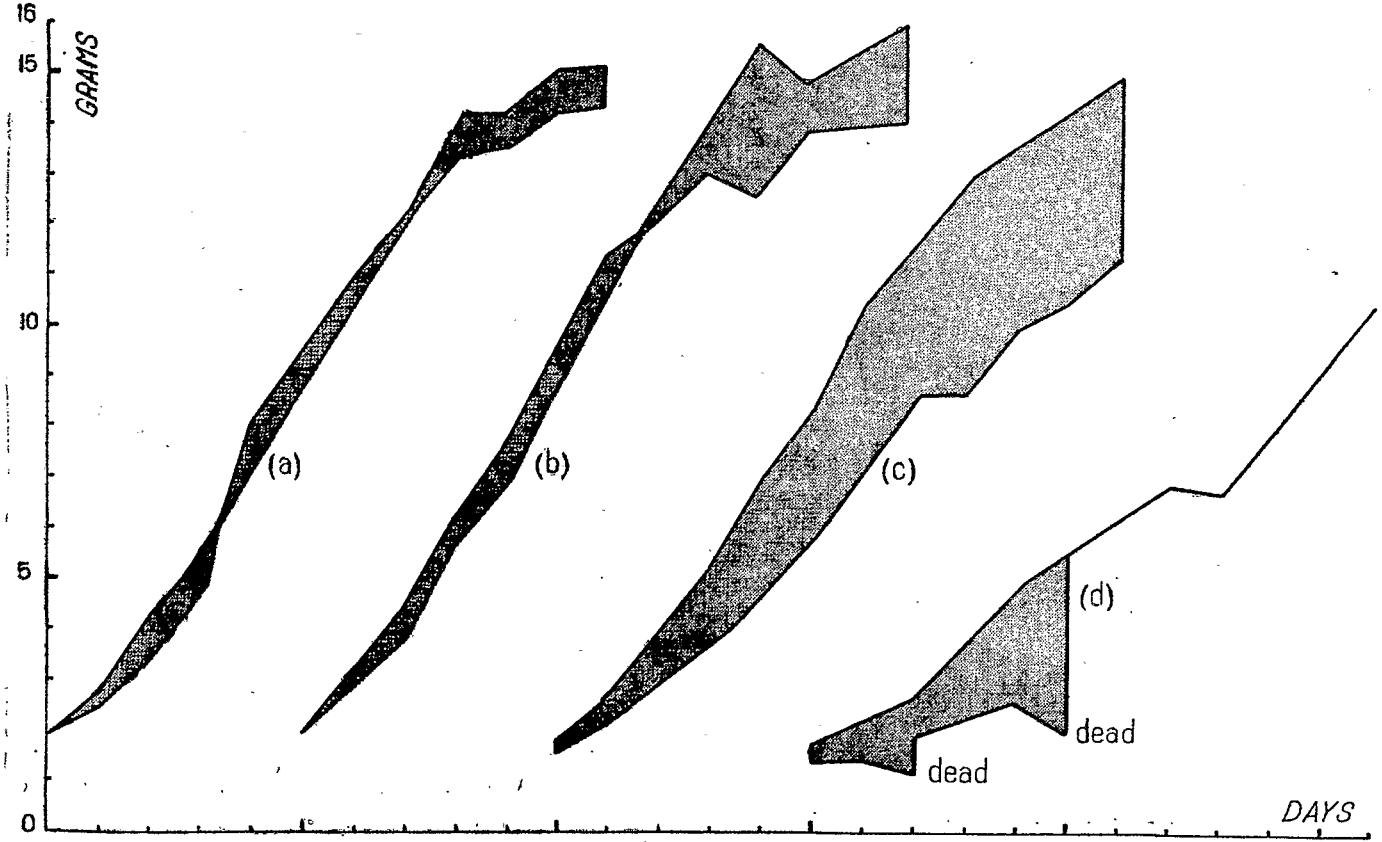


Figure 4.—Growth curves of nestlings in broods of four young, October 1956.

TABLE 5

Longevity of some banded birds.*

No.	Banded on	Recaptured on
HP 7251 ...	28. VI. 1954	26. IV. 1957
HP 7264 ...	28. VI. 1954	28. IV. 1957
HP 7431 ...	7. VII. 1954	10. V. 1957
HP 7483 ...	11. VIII. 1954	11. VI. 1957
HP 7521 ...	12. VIII. 1954	28. IV. 1957
HP 7530 ...	12. VIII. 1954	8. VI. 1957
HP 7714 ...	20. V. 1954	4. VI. 1957
HP 7804 ...	19. VIII. 1954	13. VI. 1957
HP 8028 ...	2. VI. 1954	14. VI. 1957
HP 8057 ...	15. VI. 1954	14. VI. 1957
HP 8073 ...	16. VI. 1954	25. IV. 1957 and 11. V. 1957
HP 8120 ...	18. VI. 1954	26. IV. 1957
HR 9328 ...	23. VIII. 1954	28. IV. 1957, 29. IV. 1957 6. V. 1957, 9. V. and 13. VI.
HR 9491 ...	11. II. 1955	11. VI. 1957
HR 9530 ...	3. III. 1955	13. VI. 1957
HR 9596 .	11. III. 1955	25. IV. 1957
HR 9638 ..	12. IV. 1955	13. VI. 1957
HR 9688 ...	13. V. 1955	4. VI. 1957

still present around the station in 1957. We hope to continue these banding experiments for a sufficient number of years to be able to calculate the rate of disappearance (through mortality and emigration) of the *Quelea quelea* breeding in Lake R'Kiz area.

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* All these birds were banded and recaptured at Richard-Toll

[Reprinted from the *Journal of the Bombay Natural History Society, Vol. 54, No. 4, December 1957.*]

THE BLACKFACED WEAVER BIRD OR DIOCH IN WEST AFRICA: An Ecological Study.

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