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14

Formation, sizes, and groupings of quelea nesting colonies

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Introduction

Red-billed Quelea nest in large, dense, synchronized colonies that can contain more nesting birds than colonies of any other living land bird (Lack 1968). These colonies are typically established in semi-arid savannah that has been temporarily transformed by rainfall into a luxuriant habitat with a short-lived superabundance of grass seed and insects. Quelea colonies are remarkable for the high degree of synchrony between the tens of thousands of nests, with almost all the nests being within 2 or 3 days of the same age as each other. They are also remarkable for their rapid turnover, the time from nest-building to abandonment by young being about 42 days. Records of incubation lasting 9–10 days are the shortest known for any bird (Lack 1966).

Lack (1966) found the reported nesting success of quelea (83 per cent of the eggs laid giving rise to young which left the nest) as extremely high for a small passerine. He attributed it to the comparative safety of the thorny vegetation usually used for breeding and the probable adaptive value of synchronization in 'swamping' predators. Ward (1972*b*) postulated that synchronization develops due to the simultaneous detachment of individuals in breeding condition from an overall large population consisting of individuals in all stages of breeding preparedness. Colonies may also serve as information centres on the location of patchily distributed food and water (Ward and Zahavi 1973) or as a mechanism for group cohesion and information maintenance during seasonal movements and subsequent breeding (Jaeger *et al.* 1986).

Breeding colonies are the principal targets of control operations and also have a general ornithological interest as uniquely large gatherings of land birds; yet, little has been published on colony formation, size, and groupings.

Such information is basic for developing local strategies of selective control (Chapter 22). In this chapter, we describe the areas and nest densities of ten colonies measured in Ethiopia from 1978 to 1981 and two colonies from Kenya in 1985. In addition, spatial and temporal relationships among groups of colonies in the two areas are described and the biological implications are discussed.

Measuring, sampling, and monitoring techniques

Colonies were located, mapped, and measured using techniques described by Elliott (1981*b*), Bruggers *et al.* (1981*a*), and in Chapter 4. The total number of nests in a colony was estimated either by simple random sampling of quadrats (eight colonies), stratified random sampling (one colony), or by random transects (three colonies). Quadrat size varied from 5 × 5 m in extremely dense thorny vegetation of *Acacia nilotica* to 50 × 50 m in relatively scattered *A. mellifera* thorn-bush. The number of quadrats sampled ranged from 31 (Weyto-B, Ethiopia), through 16 (Abidir, Ethiopia) and 10 (Galana-1, Kenya), to between 3 and 5 in remaining colonies.

The number of nests in each colony and the variance of the estimates for each sampling method were determined according to Seber (1973) (Table 14.1). In eleven of twelve colonies measured, productivity was determined by sampling between 40 and 1000 nests across all sampling quadrats to obtain the percentage of occupied nests. The number of nestlings per nest was determined in three colonies. Synchronization of nesting activities was estimated by ageing the oldest nestling according to Ward (1973*b*). Populations were sampled during different reproductive stages for routine data dissection as described by Ward (1973*b*).

Table 14.1. Estimating the number of nests in a colony and the sample variance (source: Seber 1973).

	Sampling method[a]	
Estimate	Random transect/random quadrat	Stratified
Number of nests	$\hat{N}=\bar{x}S$	$\hat{N}=\Sigma N_i$
Variance	$\sigma_N^2=S^2\frac{v}{s}\left(1-\frac{s}{S}\right)$	$\sigma_N^2=T_i^2\frac{v_i}{s_i}\left(1-\frac{s_i}{T_i}\right)$

[a] $\bar{x}$ = average number of nests in each quadrat sampled; S = the total number of quadrats in a colony; s = number of quadrats sampled; v = variance of quadrat counts $(x_i s)$; T_i = number of plots in the ith stratum.

Rainfall and colony formation

In Chapter 13 it was pointed out that quelea breed only during the rainy season and then only after the rains are well advanced. Rain is a critical factor in producing conditions suitable for breeding. In Ethiopia, the main rains in the southern Rift Valley occur seasonally from March through September but are most intense between July and September, and in the Middle Awash Valley they occur mainly between July and August (Jaeger *et al.* 1979). In 1981, colonies in the southern Rift Valley were installed from mid-April to the end of May. The area is drought prone, but in 1981 rainfall was plentiful (Erickson and Damena 1982).

At Galana, Kenya, the two colonies were formed near the end of a prolonged nesting season that began in the general area of Tsavo East National Park in mid-November 1984 and ended in May 1985. The peak time for colony installation in the area typically is in late December/early January, which coincides with the normal rainfall pattern. In 1984/1985, the rains beginning in October were above average and in February were three times the normal average. The latter caused a burst of annual grass seed and insect production that allowed the Galana-1 colony to be formed unseasonably late.

The conditions triggering quelea breeding are not fully understood. Disney and Marshall (1956) suggested that the onset of the rains or the greening of

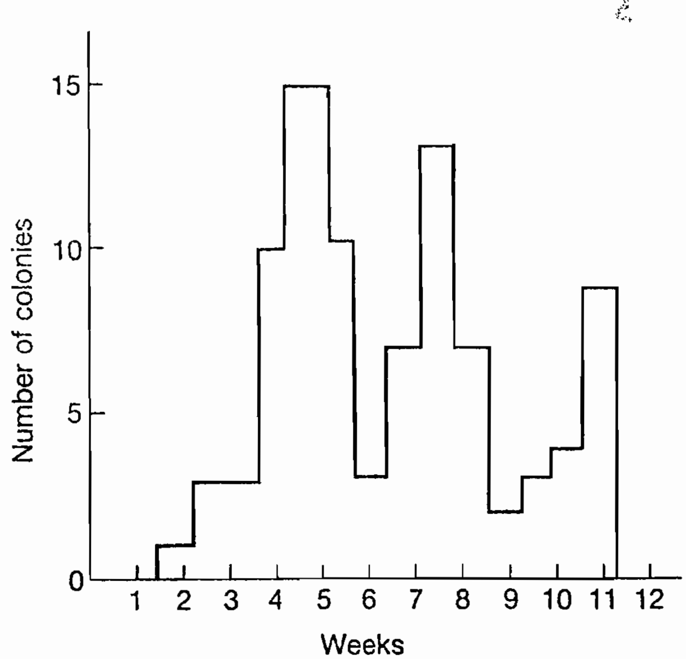

Fig. 14.1. The relationship between the number of quelea colonies installed and the elapsed number of weeks between the calculated onset of the rains and installation (source: Luder 1985*b*).

vegetation is responsible for gonadal incrudescence. Quelea need green grass leaves to construct their nests and ripening seeds and insects to feed young (Ward 1965*b*). In the Lake Chad Basin, Gaston (1973) concluded that a total of 200–450 mm of rain was necessary for the development of the annual grasses and subsequently the seeds, which form a crucial component of the food needed to support a colony. In Tanzania, Luder (1985*b*) determined that the installation dates of 72 per cent of 90 colonies were between 4–9 weeks after rainfall started (35 mm of rain falling in a 3-day period; Fig. 14.1). In this situation, colony installation peaked in the fifth and eighth weeks; a peak at 11 weeks presumably was produced by prolonged rainfall such as resulted in the Galana-1 colony in Kenya.

Nesting colony descriptions

Vegetation

The 12 colonies described here were situated in thorn-bushes or thorn-trees, most of which were 2–4 m high. Some, such as *A. nilotica*, reached 7–9 m (Table 14.2). Seven colonies were in *A. mellifera*, which is common nesting vegetation for quelea in eastern Africa (Disney and Haylock 1956; Disney and Marshall 1956); four were in other acacia species, and one was in *Terminalia brevipes*. Quelea seem to prefer the hooked thorns that make *A. mellifera* nearly impenetrable to most avian and mammalian predators (Fig. 14.2). Nests always were built within the protective tangle of thorns and from 1 m above ground to within 1 m of the tops of bushes.

In eastern Africa, quelea nesting in reed-thickets along river edges have been recorded regularly only in eastern and southern Tanzania (Kilosa and the Ruaha River at Mbarali, respectively) and in Cattail *Typha* spp. at both Lake Zwai and along the Awash River at Melkassa and Abidir (Jaeger *et al.* 1986). Colonies in tall grass such as *Sorghum macrochoeta* have only been recorded in the extreme south of Tanzania (Vesey-FitzGerald 1958). Breeding in sugar-cane has only been recorded since 1984 (near Kisumu, Kenya, C. Elliott, pers. comm.; at Joihar, NW of Mogadishu in 1987, J.-U. Heckel, pers. comm.). In western Africa, thorn-bush is also a typical nesting habitat, although colonies are regularly found in marshes of the Niger River Delta (Plate 11) and sugar-cane fields in Senegal (Morel *et al.* 1957; Ward 1965*b*).

Colony area

Quelea nesting colonies vary tremendously in size. Those reported in eastern Africa between 1978 to 1984 ($n=266$) ranged from an estimated 0.25 to 114 ha (Table 14.3). Nearly 40 per cent of these colonies were less than 10 ha,

Table 14.2. Support vegetation in quelea nesting colonies described in Ethiopia and Kenya between 1978 and 1985.

Colony	Area (ha)	Nesting vegetation: Species	Nesting vegetation: Type	Nesting vegetation: Average no./ha	Average no. active nests/ tree or bush	Sample method[a]
Ethiopia						
Weyto-B	14.0	*Acacia nubica*	Bushes, 2–4 m	NR[b]	–	RT
Weyto-D	8.1	*A. reficiens/A. nubica*	Bushes, 2–4 m	NR	–	RT
Abidir	8.0	*A. nilotica*	Trees, 7–9 m	NR	–	RT
Nura Hera	12.0	*A. mellifera*	Bushes, 2–4 m	NR	–	RQ
Awore Melka	7.0	*A. nilotica*	Trees, 7–9 m; bushes, 2.0–2.5 m	725	127	SRQ
Mulu Marsh	14.1	*Terminalia brevipes*	Trees, 3–5 m	980	48	RQ
Issa Plain	77.5	*A. mellifera*	Bushes, 2–4 m	64	40	RQ
Denku	12.1	*A. mellifera*	Bushes, 2–4 m	214	70	RQ
Omar	41.1	*A. mellifera/A. reficiens*	Bushes, 2–4 m	74	59	RQ
Kenchero	9.1	*A. mellifera/A. reficiens*	Bushes, 3–5 m	180	198	RQ
Kenya						
Galana-1	40.0	*A. senegal/A. reficiens/ A. mellifera*	Bushes, 2–4 m	143	18	RQ
Galana-2	10.0	*A. senegal/A. reficiens/ A. mellifera*	Bushes, 2–4 m	97	24	RQ

[a] RT, random transect; RQ, random quadrat; SRQ, stratified random quadrat.
[b] NR, not reported.

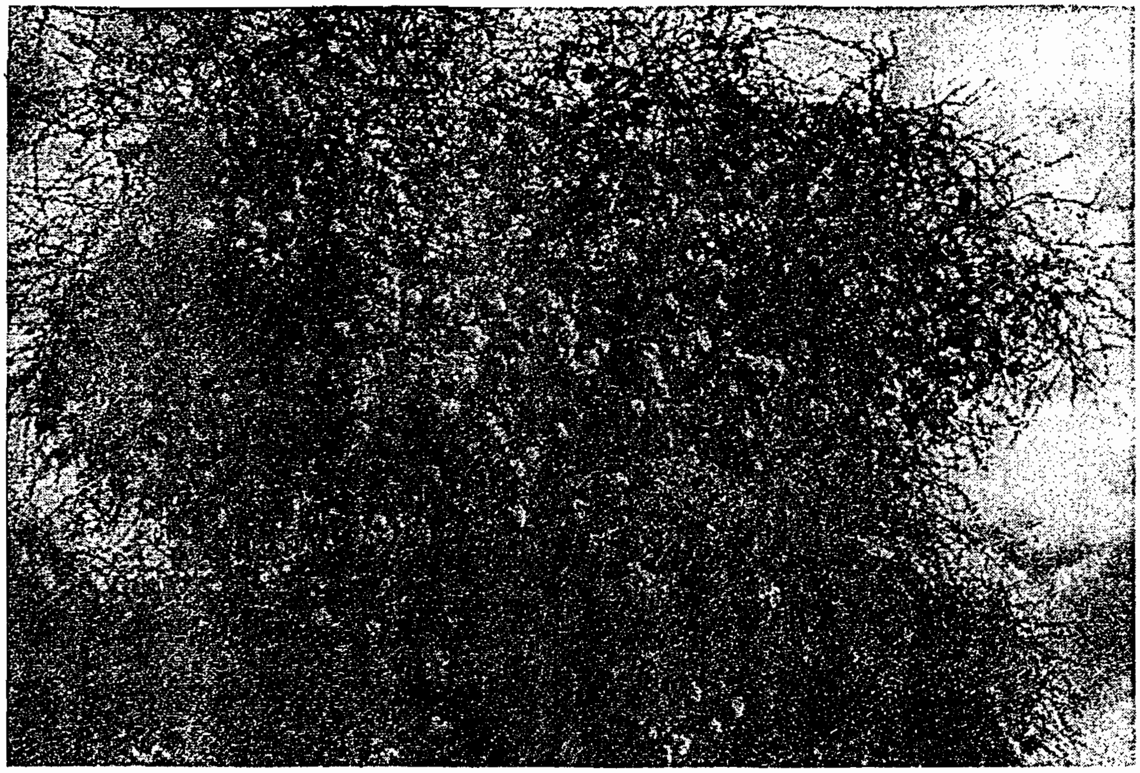

Fig. 14.2. Dense colonies are established in stands of acacia trees (photo: FAO).

Table 14.3. General description of nesting colonies of quelea in Africa (sources: FAO 1979*a*, 1980*b*, 1984*b*).

Country	Year	No. colonies	$\bar{x}$ colony area (ha) (range)	$\bar{x}$ estimated population/colony (in millions)	Support vegetation
Tanzania	1978	30	24	–	*Acacia* spp.
	1979	33	25 (3–100)	–	*Acacia* spp.
	1980	30	23 (5–114)	–	*Acacia* spp.
	1981	27	17	–	*Acacia* spp.
	1982	67	11 (0.5–60)	–	*Acacia* spp.
Ethiopia	1979	4	39 (3–80)	–	*Acacia* spp., *Typha* spp.
	1980	4	21 (10–40)	–	*Acacia* spp., *Typha* spp.
	1981	21	14 (0.25–60)	–	*Acacia* spp., *Typha* spp.
Somalia	1978–79	4	48 (12–78)	1.2	*Acacia* spp.
	1981	8	36 (10–70)	3.0	*Acacia* spp.
	1982	35	35 (10–100)	–	*Acacia* spp.
Kenya	1980	1	9	3.0	*Acacia* spp.
	1981	2	15 (10–20)	2.4	*Acacia* spp.

and about 80 per cent less than 40 ha. Our 12 colonies averaged 21 ha (7.0–77.5 ha; Table 14.2), the same average size as 7 colonies Thiollay (1978*a*) measured in Chad and Cameroon. Similarly, Ward (1965*b*) noted that colonies in Nigeria usually ranged from 15 to 30 ha. With the exception of Mali, the average size of 44 other colonies measured in Senegal, Mauritania, and Chad was similar (17–19 ha; Table 14.4).

Table 14.4. General description of nesting colonies of quelea in western Africa (source: unpubl. progress and trip reports of UNDP/FAO project RAF 73/055).

Country	Year	Colonies: No.	Colonies: Area $\bar{x}$ ha ± SD (range)	Support vegetation
Senegal	1967–77	18	17 ± 17 (1–70)	*Acacia* spp., *Typha* spp., sugar-cane
Mali	1973–77	23	63 ± 144 (1–600)	*A. senegal* *A. pennata* *A. nilotica* *A. sieberiana*
Mauritania	1967–77	16	16 ± 23 (1–80)	NR[a]
Chad	1975–78	10	19 ± 12 (3–36)	*A. nilotica*

[a] NR, not reported.

Nest density

Nest density varies widely both within and among colonies and depends mainly on vegetation species and its height and density. For example, colonies established in *A. mellifera* bushes are often large in area but contain a low nest density because bush clumps are usually scattered. Table 14.2 depicts the difference in *A. mellifera* density between the Issa Plain colony, with an average of 64 bushes/ha, and the Awore Melka colony that was continuous bush and averaged 725 trees/ha. The nest density at Awore Melka was estimated at 92 210 nests/ha compared with 2587 nests/ha on the Issa Plain (Table 14.5). Bushes in the Issa Plain colony were relatively small (2–4 m high); the mean number of nests per bush was 40 with a maximum of 161. At Kenchero, the larger bushes (3–5 m high) averaged 198 nests/bush with a maximum of 898 nests in a single bush; the estimated nest density was 35 720 nests/ha. Overall, in our 12 colonies, the average nest density among colonies was 24 954 nests/ha (Table 14.4), and the average tree density among the eight colonies where counts were made was 310 trees/ha (Table 14.2).

Table 14.5. Description of the area, number of nests, nest density, and number of breeding birds in quelea colonies sampled in Ethiopia and Kenya between 1978 and 1985.

Colony	Area (ha)	Estimated total nests	Coefficient of variation (%)	Active nests (%)	Active nests/ha	Average no. nestlings/nest	Estimated no. nesting adults[a]	Estimated no. young
Ethiopia								
Weyto-B	14.0	195 104	13	98	13 657	2.8	382 396	535 365
Weyto-D	8.1	121 759	13	95	14 280	2.7	231 336	312 312
Abidir	8.0	541 848	42	95	64 344	NR[b]	1 029 504	1 420 725
Nura Hera	12.0	71 680	51	87	5 197	NR[b]	124 728	172 118
Awore Melka	7.0	777 675	20	83	92 210	NR[b]	1 290 940	1 781 498
Mulu Marsh	14.1	783 396	22	85	47 226	NR[b]	1 331 773	1 837 847
Issa Plain	77.5	217 930	23	NR[c]	2 587	NR[b]	400 985	553 368
Denku	12.1	191 974	18	94	14 914	2.9	360 919	523 321
Omar	41.0	186 435	50	96	4 365	2.8	357 930	501 137
Kenchero	9.1	342 160	43	95	35 720	2.6	650 104	845 135
Kenya								
Galana-1	40.0	114 912	17	90	2 586	NR[b]	206 880	285 441
Galana-2	10.0	25 928	19	91	2 359	NR[b]	47 180	65 121
$\bar{x}$ (± 1 SE)	21.1 (6.16)	297 567 (75 762)		92 (1.48)	24 954 (8 419)	2.76 (0.05)	534 556 (128 312)	736 116 (176 513)

[a]Assume one male and female adult per nest.
[b]Assume 2.76 young per nest.
[c]Assume 92% occupancy.

Nest densities reported elsewhere in Africa indicated high variability among colonies. In Somalia, for instance, estimates ranged from 2892 to 8210 nests/ha among four thorn-bush colonies (J. S. Ash, in Bruggers 1980). Morel (1968) reported an average of 12 400 nests/ha in a colony in Senegal, and Thiollay (1978*a*) estimated 13 500 nests/ha among seven colonies in *A. nilotica*. In colonies located in wild sorghum and *Echinochloa* sp., Vesey-FitzGerald (1958) estimated about 5.5 nests/m^2 or 55 000 nests/ha. The highest estimate of nest density was 141 000 nests/ha in a small colony in *Typha* spp. (Fuggles-Couchman 1952 in Vesey-FitzGerald 1958), which is comparable to the highest density found in Ethiopia of 145 200 nests/ha estimated for a discrete 2.5-ha portion of the Awore Melka colony (Table 14.2).

Colony productivity

Our 12 colonies averaged 297 567 nests (Table 14.5), close to the average of 285 700 found by Thiollay (1978*a*) in Chad and Cameroon. Active nests averaged 92 per cent (range 83–98 per cent). Nesting adults ranged from 47 180 in Galana-2 to 1 331 773 at Mulu Marsh with an overall average of 534 556. Nest activity of 84–99 per cent was found in colonies in Somalia (J. S. Ash, in Bruggers 1980).

Mean clutch sizes of quelea reportedly range from 2.0 to 3.8 eggs per nest with clutches of 2.8–2.9 most common (Jarvis and Vernon, in press-*b*; Jones and Ward 1976; Thiollay 1978*a*; Ward 1965*b*). However, egg and nestling mortality occur (Chapter 16). In southern Africa, Jarvis and Vernon (in press-*b*) reported mean clutch sizes of 2.8 eggs in two colonies but only 2.1-2.4 chicks were successfully raised by each pair of adults. Three colonies in Senegal produced 2.1–2.7 young per nest (Morel *et al.* 1957). The estimated numbers of young produced in our colonies (Table 14.5) ranged from 65 121 at Galana-2 to 1 837 847 at Mulu Marsh, with an average of 736 116 per colony. Mean brood size was 2.8 young per nest. Combined numbers of adults and young averaged 1.3 million birds per colony.

Groups of colonies

Characteristics

Nesting colonies frequently occur in groups of two or more active colonies (Jaeger *et al.* 1986). The two Galana colonies in Kenya, for example, were 10 km apart, and a third colony was only 2 km from Galana-1 and 9 km from Galana-2. The Galana-1 colony was actually two adjoining colonies at different stages of development. Egg-laying was synchronous within each of these colonies but not between them. The Galana-2 colony was the most advanced, egg-laying having occurred about 1 week prior to that in the third colony, 2 weeks prior to that in the older section of Galana-1, and 3 weeks prior to that in the younger section of Galana-1. Therefore, at least four active nesting colonies occurred simultaneously within a 5-km radius.

A group of active nesting colonies might be considered a 'supercolony'. To determine whether or not there is meaning to this concept, it is necessary to know if such groups occur regularly, if they occur because of lack of suitable nesting vegetation or due to clumped food resources, and if they are comprised of a characteristic number of colonies. Multiple colony groups have been found throughout eastern Africa with group sizes of two or three colonies most common. In the Ethiopian Rift Valley, for instance, 23 nesting colonies were found in 1981 (Jaeger *et al.* 1986). Based on spatial and temporal patterns, all colonies appeared to be part of groups: five groups of two colonies, three groups of three, and one of four. Multiple colony groups have previously been recognized only as reflecting the patchy distribution of the local nesting vegetation. However, multiple colony groups also occur where nesting vegetation is continuous or in large patches, such as in the Tuli Block area of Botswana (R. Bruggers, pers. obs.). In addition, the staggered timing of colony establishment within a group, such as at Galana, suggests that the distribution of nesting vegetation is not the cause for separate colonies. On a larger scale, the distribution of nesting habitat is often patchy, and nesting colony groups can themselves be clustered. Four clusters of colonies were found, for example, in the Middle Awash River Valley of Ethiopia in 1981.

Formation of multiple colony groups

Present evidence suggests that multiple colony groups form as a succession of individual colonies from a large pre-nesting aggregation. Enormous flocks have been observed swarming in the general area when nesting colonies are being established (Ward 1972*b*). From one such pre-nesting swarm of birds located in the Weyto River Delta of southern Ethiopia in 1981 two adult male quelea were captured and outfitted with miniature radio transmitters (Bruggers *et al.* 1983). Four days later, these birds were found at a newly established colony where nest building had just begun (colony B; Tables 14.6 and 14.7). About 200 m away was a second colony (A), only 0.4 ha in size, which had been established approximately 35 days earlier. From each colony, two more adult males were instrumented with radio transmitters. Six days after colony B was established, three of the instrumented quelea were tracked to a third colony (C), 30 km to the north of B, where nest building had just begun. Colony C was smaller than colony B, and it appeared to have been formed by birds that had departed colony B 2 or 3 days earlier, leaving

Table 14.6. Listing of numbers of adult quelea (M = male; F = female) that were radio-equipped and tracked during various stages of the nesting colony cycle in the Sagon–Weyto River Delta, Ethiopia, 1981. The date and location of attachment for each bird is indicated.

Colony		Radio-equipped quelea					
Stage	Age (days)	M	Radio no.	F	Radio no.	Date instrumented	Location[a]
Pre-nesting	–	2	51, 55	0	–	17 May	Feeding flocks
Nest-building/egg-laying	1–4	2	53, 57	0	–	22 May	Colony B
	1–4	1	58	0	–	31 May	Colony C
Incubating	5–14	0	–	0	–	–	–
Care nestlings	15–24	4	60, 61, 62, 63	2	59, 64	3 June	Colony B
Care fledglings	25–43	4	65, 69, 73, 74	2	68, 72	10 June	Colony B
Adults abandoning	43	2	54, 56	0	–	22 May	Colony A

[a]Tracking dates: Helicopter — 17, 18, 21, 22, 23, 25, 26, 28, 30 and 31 May; 3, 5, 8, 10, 11, 12, 15, 19, 20, 22, 24, 25, 27, and 28 June; ground — 22, 26, 28, and 31 May; 3, 5, 8, 10, 11, 12, 19, 20, 24, 25, 27, and 28 June.

Table 14.7. Description and chronology of four quelea nesting colonies found in the same area in the Sagon–Weyto River Delta, Ethiopia, 1981.

Colony	Location	Area (ha)	Estimated no. completed nests/colony	% nests occupied	Average no. eggs/nest	Estimated population ($\bar{x}$ 1000)		Approximate date	
						Adults	Young	Nest construction	Colony dispersal
A	5°01′ N × 36°58′ E	0.4	20 000	40–50[a]	Not determined	1–2	3–5	13–15 Apr.	1–2 June
B	5°01′ N × 36°57′ E	14.0	196 000	98	2.82	464	560	19–21 May	28–30 June
C	5°16′ N × 37°03′ E	2.1	1 652	0	0.00[b]	50–80	0	27–29 May	28–30 May
D	4°59′ N × 36°58′ E	8.1	120 176	95	2.70	240	247	30 May–2 June	10–12 July

[a] Estimated from the presence of droppings in nests.
[b] Colony abandoned before laying completed.

behind many unfinished or unoccupied nests. Colony C was completely abandoned after 3 days, possibly due to the disappearance of nearby water. The three instrumented quelea were then tracked to a fourth colony (D), 5 km from colonies A and B, where nest building was underway. Colony D later appeared to be two adjoining colonies, 3 days out of phase with one another. These findings suggest that colonies B and D were formed successively over a 10-day period by splitting of the original pre-nesting aggregation. Both colonies were successfully completed.

Unoccupied nests along the periphery are a common feature of quelea colonies. Ward (1965*b*) assumed that these unused nests resulted from colony contraction as its centre becomes defined, and birds abandon peripheral sites for more central ones. We found that the quelea that left colony B were not ready to breed, suggesting that multiple colony formation results from a stepwise sorting of birds in similar reproductive condition into individually synchronous colonies.

Reproductive synchrony within quelea colonies, or sections of colonies,

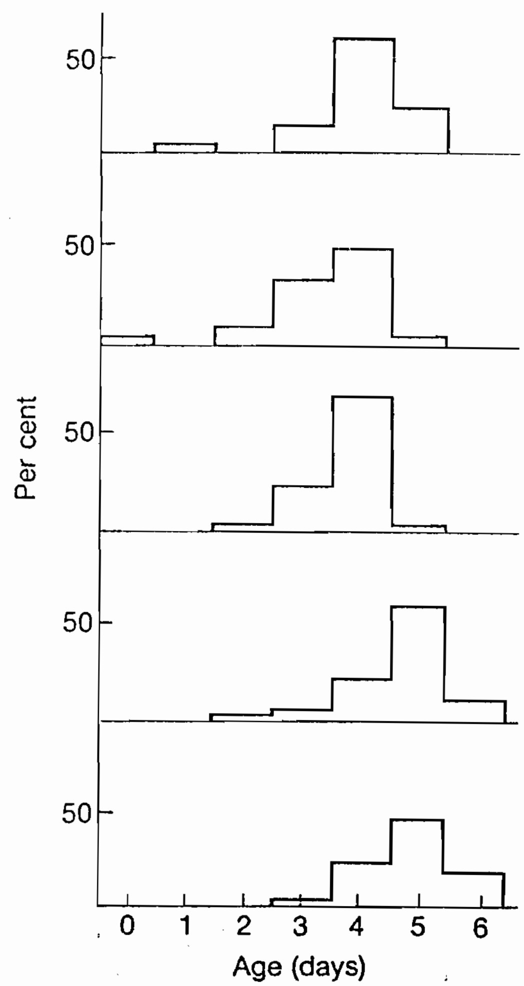

Fig. 14.3. Age of largest nestling from 100 nests in each of five randomly selected blocks of colony B in the southern Rift Valley, Ethiopia, 10 June 1981.

has been well documented. The synchrony of nestling development in colony B is illustrated in Fig. 14.3. Although the average age of the largest nestling from each of the five different areas on 10 June was significantly different ($P<0.05$), the age range was only 0.8 day ($\bar{x}=4.1$–4.9 days of age) across areas. Adult females sampled from both the pre-nesting aggregation and from colony B on the day preceding onset of egg-laying and prior to the formation of colony C were more asynchronous in their follicle development (Fig. 14.4). From those collected at colony B, approximately 60 per cent had follicles of 4–9 mm in length, indicating that they might soon lay eggs. A similar pattern was found in a sample of pre-nesting females collected at about the same time along the Omo River. Ward (1965*b*) also noted a lack of synchronization of pre-nuptial moult and gonad size in a pre-nesting aggregation of quelea.

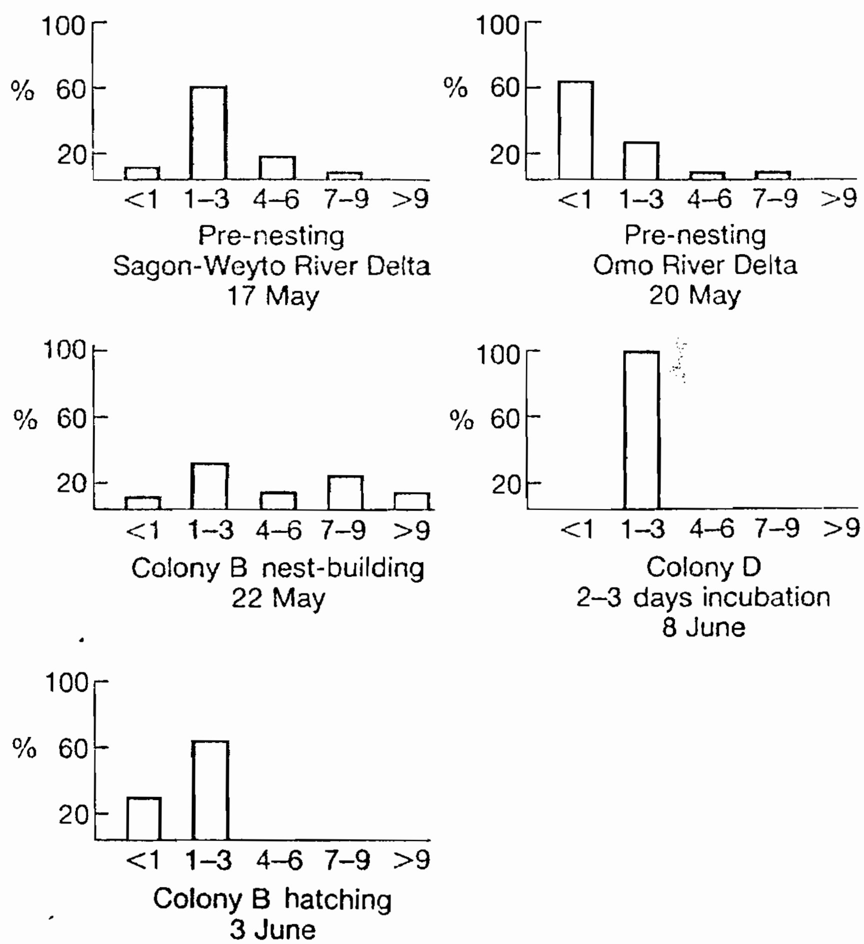

Fig. 14.4. Percentage quelea females with largest follicles in various size classes between 1 and 19 mm in length. Birds were collected in pre-nesting flocks or from inside colonies during the different developmental stages in southern Rift Valley, Ethiopia, 1981 ($n=50$–159 birds/collection).

Roosts associated with nesting colonies

Non-breeding quelea

Non-breeding adults will join a night roost occurring at a colony during its formative stage, as we described for colony B; but, presumably, these non-breeding birds depart to roost elsewhere as egg-laying and incubation begin. Their departure may be due to a general breakdown in roosting behaviour resulting from breeding birds becoming more attentive to their clutches. The behaviour of post-breeding adults towards nearby nesting colonies can vary. For example, radio-equipped adults from colony A did not immediately depart the area, but instead moved and roosted with other birds near the three other colonies. One was found at a night roost near colony C the day before that colony was discovered, and then for a short time in colonies C and D. In contrast, of nine adult quelea that were instrumented during the post-breeding stage in Galana-2 colony at the time of its completion, none were later found at the two younger colonies nearby.

Juveniles often remain in the vicinity of nesting colonies for days and sometimes weeks after adults depart. This segregation from adults can be maintained for months following breeding (Jaeger *et al.* 1979). Because of this tendency for post-breeding segregation, we assume that juveniles do not generally attach themselves to other nearby colonies. Juveniles from colony A were not found in later samples from either colonies B or D, although some were collected from the short-lived colony C. One to two months after breeding in this general area of southern Ethiopia, the adults migrated north into the Awash River Valley to breed a second time (Jaeger *et al.* 1986). Only a small percentage of the quelea collected in the Awash colonies were juveniles that had been produced earlier in the south. Many of these juveniles had begun moulting directly into adult breeding plumage and had interrupted the post-juvenile moult of the primaries. Adults that were nesting for the second time had also interrupted the post-breeding moult of the primaries. Juvenile males had enlarging testes but juvenile females, in contrast to adults, had small follicles. J. Thompson and M. Jaeger (unpubl. data) have found evidence in Kenya for breeding by quelea that have not yet completed the post-juvenile moult.

Late-colony roosts

Roosting and flocking behaviour by adults reappears in the late stages of breeding, a week or two before adults depart a colony. This is most pronounced with males and becomes apparent when young begin flying. At this time, night roosts of adults are commonly formed away from the colony. During the late fledgling stage of colony B, four radio-equipped adults were found using a night roosting site about 1 km from the colony. Late-colony roosts of adults are also found within colonies. The Galana-1 colony had a very large roost within it that appeared to include adults from the older colony nearby.

Biological implications

Synchrony is the most consistent feature of the colonies discussed in this chapter. The potential adaptive advantages of synchrony are generally attributed to minimizing losses to predators (Lack 1968) or improving communal food finding by young (Ward and Zahavi 1973). In addition to these functions, synchrony may be important for maintaining group cohesiveness for successive breeding. Results from marking studies in Ethiopia suggested that post-nesting group cohesion of adults exists and that these groups migrate independently of each other (Jaeger *et al.* 1986). P. Jones (pers. comm.) reported that quelea ringed in South Africa were captured together after a period of 18 months.

The biological implications of multiple colony groups also are intrigueing. These groups may result from the strong tendency for reproductive synchrony of birds within individual colonies. The finding of a supercolony whose components are out of reproductive synchrony with one another, further suggests that the role of synchrony may be more complex than simply minimizing the time spent nesting in an area to reduce the potential impact by predators (Jaeger *et al.* 1986). If, for instance, all quelea in an area nest in the same colony, it may increase the risk of overall failure. This could easily have happened if all birds in the Weyto–Sagon River Delta in Ethiopia in 1981 had tried to nest near the location where colony C was attempted and later abandoned due to drying up of the standing water, desiccation of grasses, and subsequent lack of insects. Therefore, one potential advantage of birds nesting in multiple colony groups dispersed in time and space may be to increase the chances of some of the colonies in the area being successful. This, in fact, was the situation in the Weyto–Sagon area.

Management implications

Surveys for quelea nesting colonies can be done more efficiently with an understanding of the vegetation and topography that characterize nesting sites. Nesting vegetation will vary with habitat; for instance, where marshes predominate or dense acacia is absent, colonies are commonly in *Typha* spp. Throughout much of their range, however, quelea nest in semi-arid savannah where colonies usually occur in discrete patches of *Acacia* sp. thorn-bush along seasonal drainages and often at the base of a slope where grass growth is relatively pronounced (Chapter 4). These patches of thorn-bush are easy to recognize from the air by an experienced observer. In addition, nesting colonies tend to re-occur in the same areas each year, if food conditions are favourable (Jaeger *et al.* 1986). Therefore, it is useful to keep accurate records of the locations of nesting colonies on maps or aerial photographs.

Nesting colonies frequently occur in groups of two or three, so that where one is found, survey efforts should be intensified as others probably also occur. Radio-telemetry can be useful for locating colonies in rough terrain (Chapter 6; Bruggers *et al.* 1983) or sufficiently early during their establishment to permit control to be conducted prior to young fledging (after which non-target predatory birds become more numerous [Bruggers *et al.*, in press]) and adults begin departing the colony.

Nesting colonies show great variability in size, nest density, and bird numbers. Therefore, not all colonies are of equal value to control. Often the success of a control campaign is based on the number of colonies sprayed and the volume of avicide used, measures which probably bear little relationship to the numbers of birds sprayed or the amount of crop saved. As an example, the largest colonies measured here (Table 14.4) in terms of area were among the smallest in numbers of nesting adults, and vice versa ($r = 0.25$, not significant). A better indicator of the number of nesting adults was nest density/ha ($r = 0.91$, $P < 0.001$). Generally, aerial spraying is more effective on the smaller and more densely populated colonies. Nesting quelea scatter away from the colony after only two or three passes of the spray aircraft so that additional passes required of larger areas have less and less effect. Large colonies often require two or more nights of spraying for a satisfactory result. Aerial spraying then becomes less efficient as colonies get larger in area and lower in bird density. Aerial spraying of colonies is more effective if directed against the moving mass of birds as opposed to spraying colony swaths.

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