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Distribution, populations, and migration patterns of quelea in eastern Africa

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Introduction

Developing effective strategies for selective control of the Red-billed Quelea *Quelea quelea* depends on understanding their seasonal distribution in relation to that of susceptible cereals (Dyer and Ward 1977). Based on this information, control can be focused on only those quelea concentrations likely to do damage. Where possible, control can be directed against nesting colonies before quelea disperse and move into cereal-growing areas.

Biogeographical research has been an important part of quelea projects in eastern Africa since 1968. Four geographical races of quelea were proposed for the region with only *Q. q. aethiopica* (Sundevall) and *Q. q. intermedia* (Van Someren) posing important threats to cereals (Ward 1971; Fig. 10.1). The *Q. q. intermedia* race was believed to migrate back and forth between central Tanzania and southern Somalia (Figs. 10.2 and 10.3) following the rainfront as it moves north and south across the equator (Ward 1971). It was considered that breeding occurred wherever favourable conditions were encountered, that locations could change from year to year depending on the pattern of favourable rainfall, and that in years of widespread rain the same birds could breed as many as five times in five different areas.

Ward (1971) proposed the same general model for *Q. q. aethiopica* migrations to the north (i.e. migration following the rainfront), but acknowledged that little was actually known about these quelea, particularly in Ethiopia and northern Somalia.

In 1979, a UNDP/FAO regional quelea project was established to monitor the seasonal distribution and movement patterns of *Q. q. aethiopica* and *Q. q. intermedia*. Timely reporting was considered essential for coordinated re-

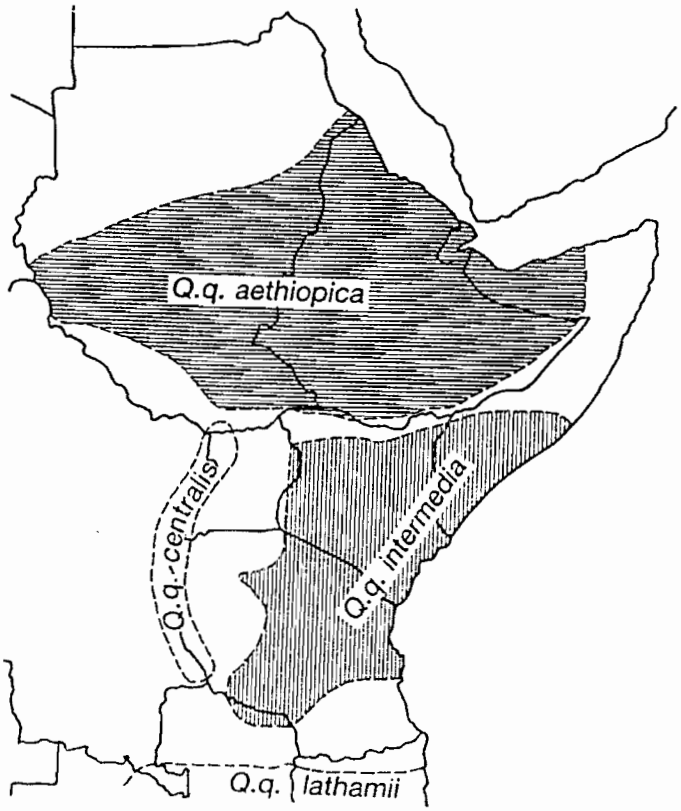

Fig. 10.1. The approximate distribution of races of *Quelea quelea* in eastern Africa, as proposed by Ward (1971).

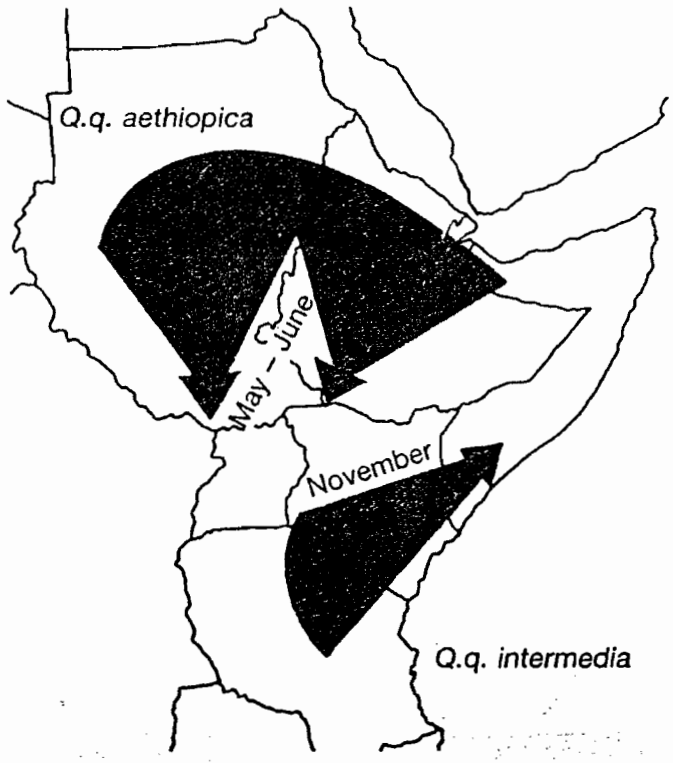

Fig. 10.2. The 'early-rains migration' routes of the *Q. q. aethiopica* and *Q. q. intermedia* races in eastern Africa, as proposed by Ward (1971).

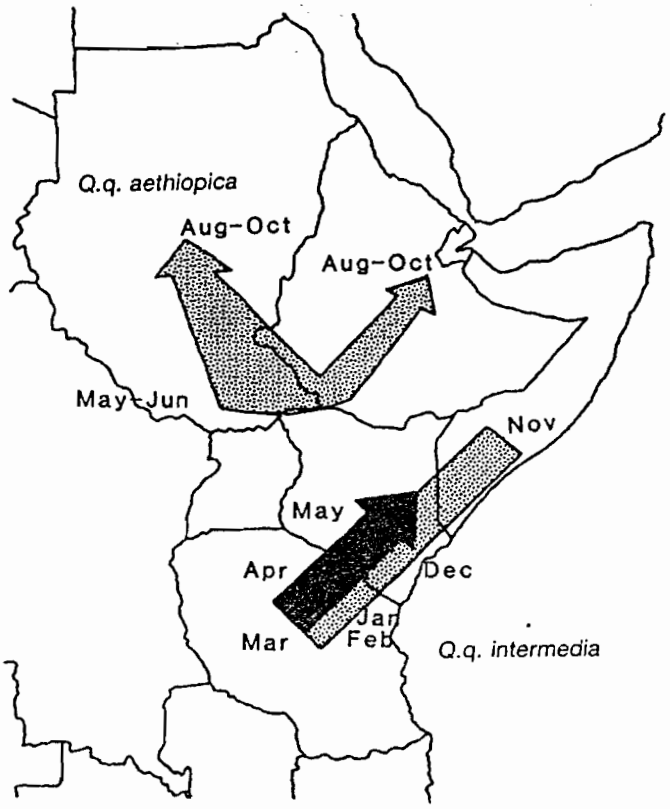

Fig. 10.3. The 'breeding migration' routes of the *Q. q. aethiopica* and *Q. q. intermedia* races in eastern Africa, as proposed by Ward (1971). The black arrow illustrates the return 'breeding migration'. The route shown for Ethiopia was predicted by Ward (M. Jaeger, pers. comm.) subsequent to the 1971 publication.

gional control of these two populations before quelea outbreaks in areas of ripening cereals. The quelea problem in eastern Africa was viewed as being analogous to that of the Desert Locust *Schistocerca gregaria* swarms where regional control could be restricted to clearly defined source areas.

An operational programme for regional monitoring and control at the population level, however, has not been realized, owing to the complex nature of quelea movements within the region. Present information suggests that there are three or more populations that intermix within the range of Ward's *Q. q. aethiopica* and *Q. q. intermedia*; that within populations nesting is widely scattered in both time and space; and that migratory movements are fragmented as opposed to massed. We will review the evidence upon which these observations are based, discuss how this information has changed our perception of the quelea problem, and suggest ways to approach its solution.

Surveys and methods

Quelea have been sampled over much of eastern Africa since 1950, but in

general, this sampling has not been systematic. Consequently, quelea populations, their migratory movements, and the occurrence of breeding are unknown in many areas. This is due, in part, to the difficulties involved in getting to remote areas during the rains. Since 1978, when helicopter surveys began, considerable information has been obtained on the location and timing of quelea nesting. Quelea have been most thoroughly sampled in the Ethiopian Rift Valley (Bruggers *et al.* 1983; Erickson 1979; Jaeger *et al.* 1986; Jaeger and Erickson 1980; Jaeger *et al.* 1979) and in Tanzania (Disney and Haylock 1956; Disney and Marshall 1956; Elliott 1983*a*; Luder 1985*a*; Luder and Elliott 1984; Vesey-FitzGerald 1958; Ward 1971; Ward and Jones 1977). Data also are available from eastern Kenya (Allan 1983; J. Thompson and M. Jaeger, unpubl. data) and from southern Somalia (Ash and Miskell 1983; Bruggers 1980). The data collected through 1981 have been tabulated in Jaeger *et al.* 1981. Potentially important areas from where little or no information is available include southern Sudan, northern and south-eastern Ethiopia, western and north-eastern Kenya, south-western Somalia, western Tanzania, and Uganda.

For each sample taken since 1980, a population 'fingerprint' was prepared (Jaeger *et al.* 1986; Chapter 4) for male mask index, stage of cranial pneumatization, progress of post-juvenile or post-breeding primary moult, interrupted primary moult, and gonad condition (see Ward 1973*b* for a description of these methods). Quelea are polytypic for the extent of the black facial mask of males (Ward 1966, 1973*b*). 'Fingerprint' data can permit determination of (1) the occurrence and timing of nesting within the previous 6 months, and (2) the geographical population to which the sample is affiliated. When taken together with knowledge of the spatial and temporal pattern of nesting, it can be used to determine when and from where a particular group of quelea is likely to have come.

Distribution

Spatial

The known distribution of quelea habitat in eastern Africa is illustrated in Fig. 10.4. It includes central Sudan, the Rift system, and a broad swath extending from southern Tanzania north-east through Kenya to southern Somalia (Allan 1983; Ash and Miskell 1983; Bruggers 1980; Bruggers and Jaeger 1982; Bruggers *et al.* 1983; Disney and Haylock 1956; Disney and Marshall 1956; Elliott 1983*a*; Erickson 1979; Hall and Moreau 1970; Jaeger *et al.* 1986; Jaeger and Erickson 1980; Jaeger *et al.* 1979; Magor and Ward 1972; Urban and Brown 1971; Vesey-FitzGerald 1958; Ward 1971; Ward and Jones 1977; Williams 1954). In Sudan, the quelea's range is retreating to the south because of desertification and the destruction of thornbush for large-scale farming. Figure 10.5 gives the distribution of quelea breeding

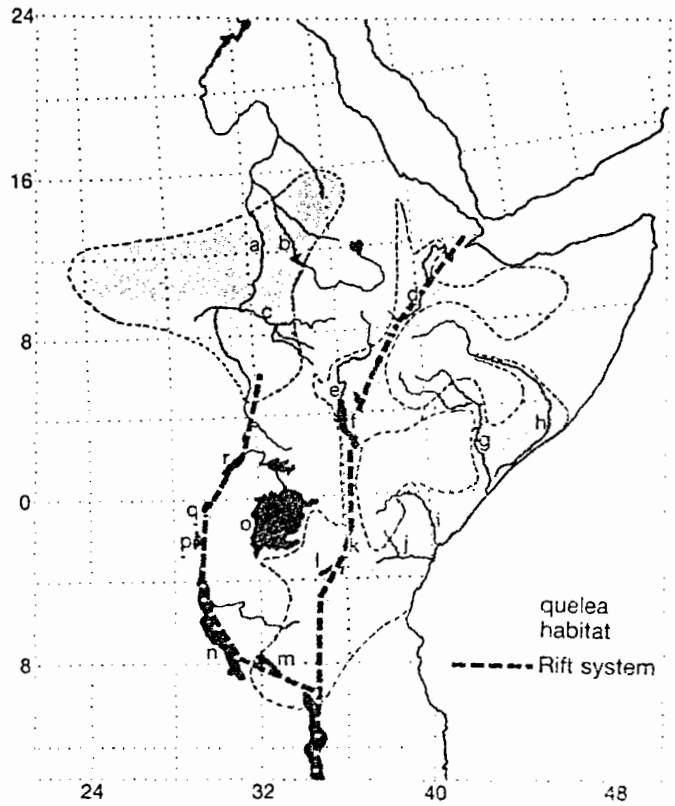

Fig. 10.4. The known distribution of quelea habitat (shaded areas) in eastern Africa. Major rivers and lakes include *a*, White Nile; *b*, Blue Nile; *c*, Sobat; *d*, Awash; *e*, Omo; *f*, Turkana; *g*, Juba; *h*, Webi Shebelli; *i*, Tana; *j*, Galana; *k*, Natron-Magadi; *l*, Iyasie; *m*, Ruhkwa; *n*, Tanganyika; *o*, Victoria; *p*, Kivu; *q*, Idi Amin; *r*, Mobutu.

records from within the region. The greatest number of nesting colonies reported each year are from control operations in Sudan and Tanzania. Sufficient data are not available to allow statistically reliable estimates of population numbers, as surveys for nesting colonies are neither comprehensive nor systematic.

Temporal

The seasonal movements and breeding of quelea are closely tied to movement of the rainfront (Intertropical Convergence Zone) and the subsequent production of grass seeds (Chapter 9; Elliott 1979; Jaeger *et al.* 1986; Jaeger *et al.* 1979; Ward 1965*a*,*b*; Ward and Jones 1977). The array of physiographic features within the region, such as the mountains and lakes associated with the Rift system, together with proximity to the equator and Indian Ocean results in a complex pattern of rainfall (Brown and Britton 1980; Brown *et al.* 1982). Consequently, quelea nesting can occur somewhere within the region throughout most of the year and simultaneously at two or more widely separated locations.

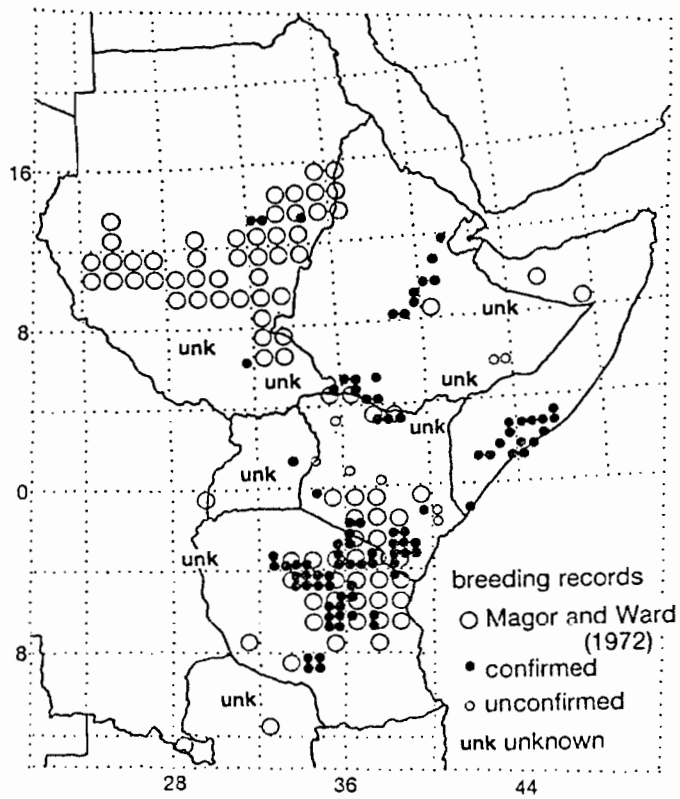

Fig. 10.5. The distribution of breeding records of *Quelea quelea* in eastern Africa. Small circles are records with 1/2° grid squares, while larger circles represent records by 1° grid squares.

Figure 10.6 illustrates the months and general areas where evidence of quelea nesting has been found since 1978. The general trend is for two separate nesting seasons nearer the equator (May–June and Dec.–Jan.), particularly in eastern Kenya and southern Somalia where a bimodal rainfall pattern is more evident (rainfall regions D and E; Brown and Britton 1980). Nesting has also been found during August and September near the coasts of southern Somalia and northern Kenya; but it is not known how regularly this occurs. In the remainder of the region there is normally a northward wave of nesting beginning earlier to the south (southern Tanzania, Feb.–Mar.) and ending later to the north (central Sudan, Sept.–Oct.). This scheme, however, does not include the Rift Valley lakes of western Uganda and western Tanzania where little is known about quelea nesting.

In eastern Africa, the same quelea can breed two or more times in a year. Opportunities for multiple breeding can occur both within and between breeding seasons. Within a nesting season successive breeding can occur in two ways. The more common way probably is itinerant breeding (Ward 1971) where adults depart from a successfully completed colony, follow the rainfront, and re-nest hundreds of kilometres away where later-maturing grasses are green and ripening. The best evidence for itinerant breeding is

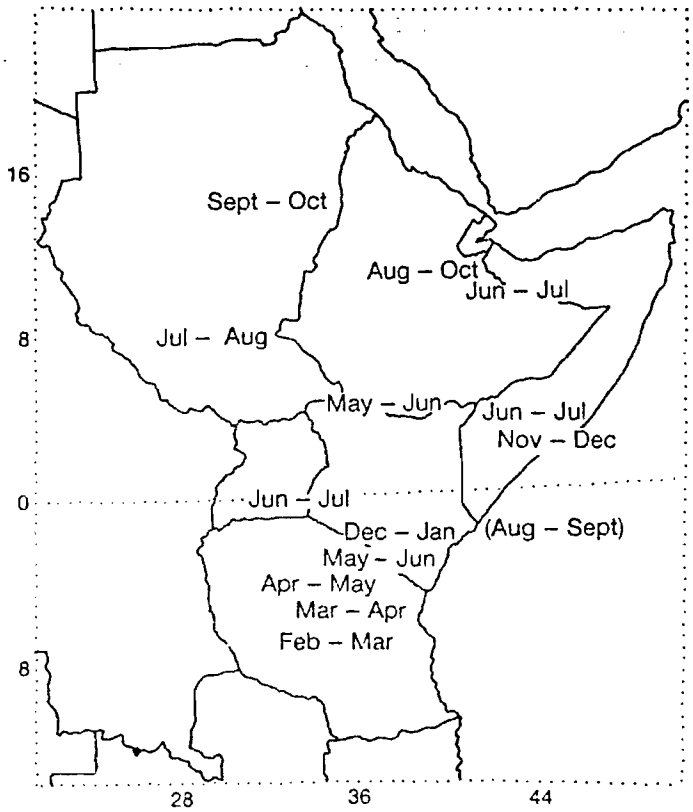

Fig. 10.6. The known temporal distribution of quelea breeding in eastern Africa. This is not to suggest that nesting occurs at these times and places each year, but that it regularly occurs when rainfall is sufficient. Parentheses indicate that nesting at this time and place may not be a regular occurrence.

from the Ethiopian Rift Valley (Jaeger *et al.* 1986) where adults, colour-marked at colonies in the southern Rift during June 1981, were recovered in September at colonies 500–700 km to the north in the Awash River Valley. Indirect evidence from 'fingerprinting' samples suggests a similar occurrence in Tanzania where quelea nesting during February and March in central Tanzania can move north to re-nest during May and June in north-eastern Tanzania.

A second form of successive breeding occurs with re-nesting in the same general area in response to prolonged rains. Strong evidence for this has been found in south-eastern Kenya where nesting colonies were found in the vicinity of Tsavo East National Park from December 1984 to June 1985. Adults, colour-marked at one nesting colony in January, were recovered at another colony 125 km to the east in late March (J. Thompson and M. Jaeger, unpubl. data). In central and southern Tanzania, breeding sometimes occurs over a 3-month period (C. Elliott, pers. obs.), allowing the possibility for successive breeding by the same individuals. However, this has yet to be substantiated. At present, there is no compelling evidence of three or more nestings in succession, although the opportunities seem to exist in the south-

east (Feb.–Mar., May–June, Aug.–Sept., and Dec.–Jan.; Fig. 10.6). Here quelea can also nest in the same area in two separate seasons (May–June and Dec.–Jan.). Figure 10.7 illustrates possible opportunities for multiple breeding within the region.

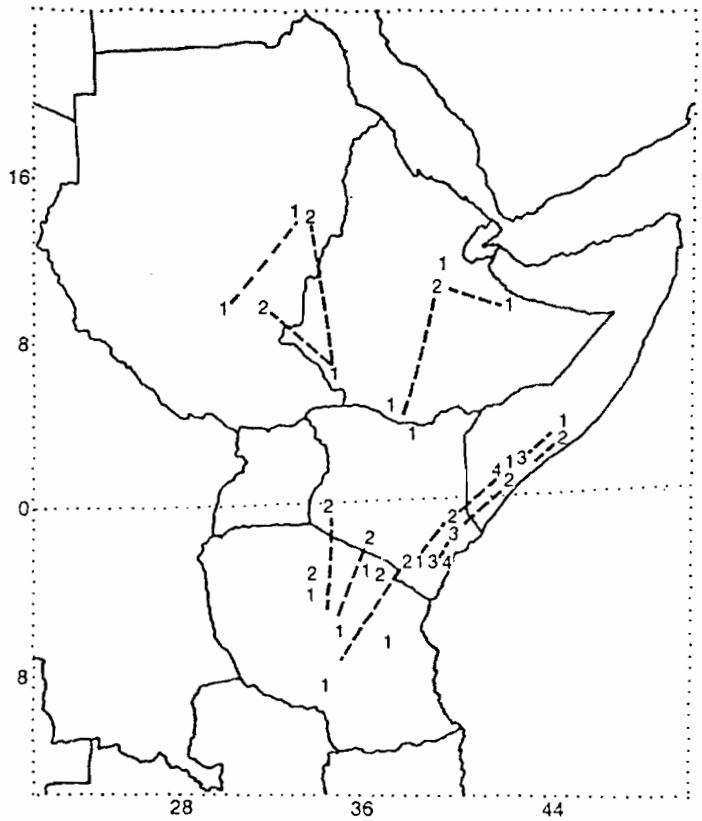

Fig. 10.7. The known opportunities for multiple breeding by quelea in eastern Africa within the same year. Numbers 1–4 represent first to fourth breeding by the same birds. In some situations, birds nesting for the first time may do so in an area with birds that have nested earlier.

Populations

As a basis for understanding quelea movements in eastern Africa it was first necessary to determine whether discrete populations or races of quelea exist, and if so, to determine the limits of their distribution. Ward (1966) compared geographical variation in several characters of the colour pattern of males in breeding plumage. He concluded that in eastern Africa only one valid race *Q. q. aethiopica* existed, distributed through the savannahs of Sudan, Ethiopia, and northern Somalia and that the rest of the region was populated by a hybrid swarm of *Q. q. aethiopica* and the *Q. q. lathamii* (Smith) race of southern Africa. Ward decided at that time that the *Q. q. intermedia* race, proposed by Van Someren (1922) to describe the quelea of Tanzania and

adjacent areas, should be rejected because of its high variability. For similar reasons he also rejected the *Q. q. centralis* (Van Someren) race of the Rift Valley of western Uganda, Rwanda, Burundi, and western Tanzania. Later (Ward 1971) larger samples from Kenya and Tanzania convinced him that *Q. q. intermedia* was after all valid because it was so distinct from both *Q. q. lathamii* and *Q. q. aethiopica* despite its variability. Data supporting this conclusion were never published.

The *Q. q. aethiopica* and *Q. q. intermedia* races postulated by Ward (1971) now seem to be an oversimplification of the pattern of quelea distribution and intermixing in eastern Africa. These distinctions were based largely on the composition of male mask types from relatively few samples of restricted distribution. For instance, large samples had not been collected from Ethiopia or northern Somalia. Since then, more than 26 000 masks from a much wider variety of sampling sites have been examined. Figure 10.8*a* shows the percentage of males with little or no black frontal band (mask types 1 and 2) from pooled samples collected from 1978 to 1985. A geographical gradient in the composition of mask scores is apparent, with the highest percentage of frontal bands to the south-east and the lowest to the north-west (Sudan). This follows the general pattern of the cline suggested by Ward (1966), with increasing percentages of frontal bands to the south and to the west, so that samples from South Africa and Senegal, respectively, are almost exclusively of males with broad frontal bands (mask type 7).

The distribution of mask types illustrated in Fig. 10.8*a* suggests that the cline is broken into at least three local populations, or demes (Endler 1977; Mayr 1971) within eastern Africa: (1) Sudan, (2) the Ethiopian Rift Valley and adjoining areas, and (3) Tanzania, eastern Kenya, southern Somalia. The population in Sudan (95–97 per cent mask types 1 and 2, Fig. 10.8*a*) has been the least sampled, particularly in the south; nevertheless, it seems to be physically separated from the population in the Ethiopian Rift Valley by the highland plateau forming the Rift. Regular exchange probably takes place across south-western Ethiopia.

The population centred in the Ethiopian Rift Valley (85–87 per cent) includes quelea to the east in the northern Ogaden (84 per cent) and to the south into Kenya (79 per cent). An unconfirmed report of quelea nesting colonies in the Kenya Rift Valley at Lodwar on the south end of Lake Turkana (Fig. 10.4) and at Lake Baringo in the central Rift in 1986 (F. Kitonyo, pers. comm.) may explain the different mask index found in central Kenya (72 per cent from Fig. 10.8*a* and 77 per cent from Fig. 10.8*b*). This may be a fourth population distinct from that in the Ethiopian Rift; further sampling is needed to clarify the matter. The third population from Tanzania (53–55 per cent), eastern Kenya (46 per cent), and southern Somalia (56 per cent) seems to form a distinct unit (*Q. q. intermedia*), as suggested by Ward (1971), except that the Kenya percentage is lower than the other two (Fig.

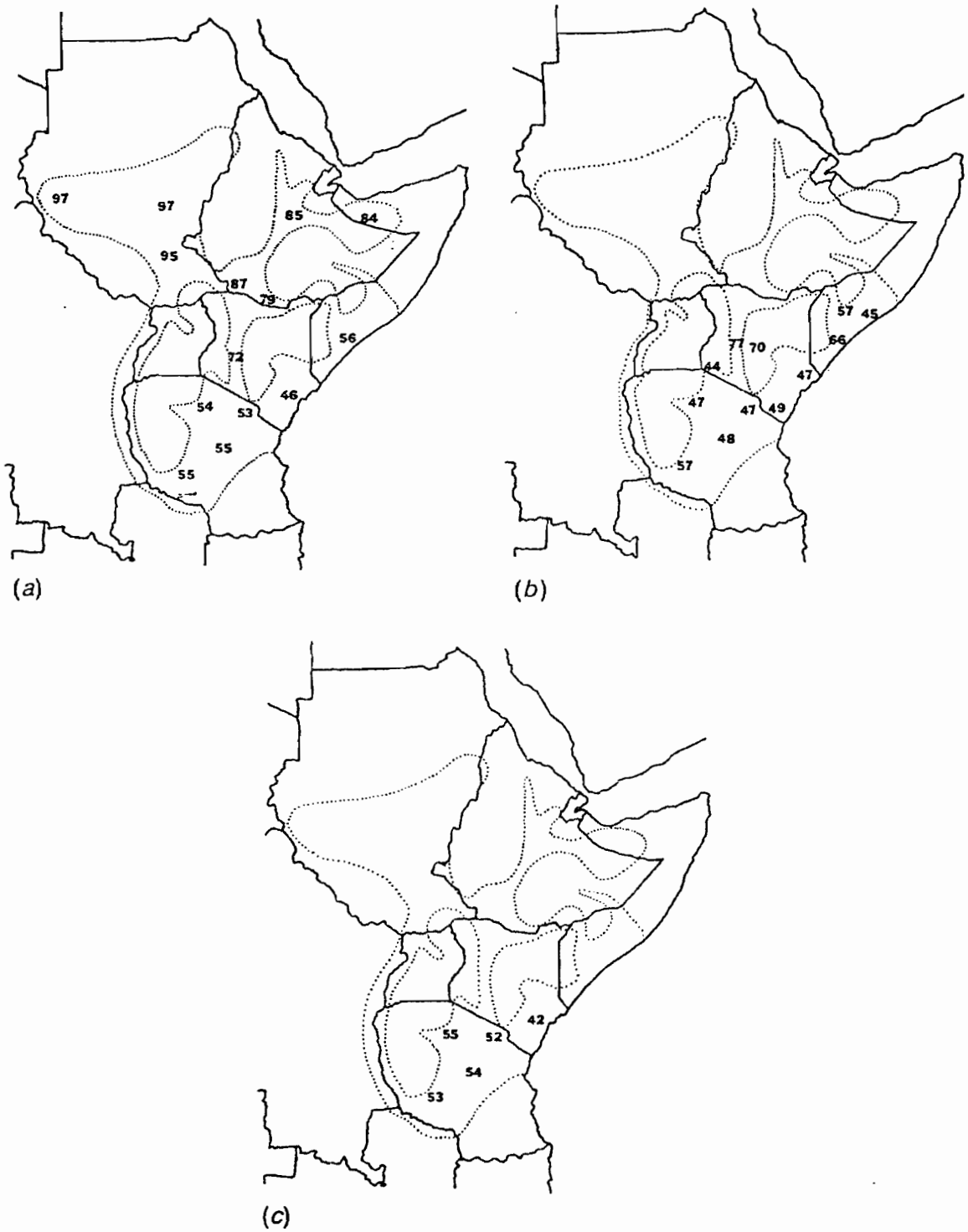

Fig. 10.8*a*. The distribution of male facial mask scores (per cent 1 and 2, no frontal band) from samples pooled over all years ($n = 26\,123$) in eastern Africa. (See Chapter 4 for facial mask score technique.)

Fig. 10.8*b*. The distribution of male facial mask scores (per cent 1 and 2, no frontal band) from samples from 1984 ($n = 5401$) in eastern Africa. (See Chapter 4 for facial mask score technique.)

Fig. 10.8*c*. The distribution of male facial mask scores (per cent 1 and 2, no frontal band) from samples from 1985 ($n = 3111$) in eastern Africa. (See Chapter 4 for facial mask score technique.)

10.8*a*). In early 1984, a drought affected the region and was particularly severe in Kenya. Figure 10.8*b* shows that in that year, mask index percentages were lower than usual in Tanzania, implying more intermixing with birds from Kenya. At the same time they were higher than usual in Somalia, indicating possible intermixing also with birds from Ethiopia. In 1985 (Fig. 10.8*c*), the pattern of a distinct difference between Kenya and Tanzania was re-established. The *Q. q. intermedia* population may, therefore, be split into sub-populations in Tanzania, Kenya, and Somalia with climatic conditions increasing or decreasing the amount of mixing.

Another population may also have an influence on the region. This is *Q. q. centralis* which is said to inhabit a restricted area of grassland associated with the Rift Valley lakes of Mobutu, Idi Amin, Kivu, and Tanganyika (Fig. 10.4; Ward 1971). Very little is known about quelea in this area. However, they may intermix with the populations in Sudan and Tanzania as indicated in Figs. 10.8*a* and 10.8*b*.

The above information indicates that the subspecies designations *Q. q. intermedia* and *Q. q. aethiopica* (Ward 1971) are unapplicable to the more complex and dynamic situation existing within the region and that, as such, use of subspecies designations should be discontinued. Clines in geographical character variation, as occur for quelea in eastern Africa, also occur in other passerines; for example, Red-winged Blackbirds *Agelaius phoeniceus* (James 1983; James *et al.* 1984; Power 1970) and House Sparrows *Passer domesticus* (Johnston 1969; Johnston and Klitz 1977; Selander and Johnston 1967).

Seasonal movements

Sudan

Ward (1971) suggested that quelea across Sudan migrate along a north-south axis approximately between 13° and 4° N. The main dry-season quelea concentrations are reported between 13° and 9° N (Bruggers *et al.* 1984*a*; Ward 1971). According to Ward's model, as the rainfront progresses northward, quelea undertake an early-rains migration southward in June into the rains where fresh grass seed is available. These birds are believed to nest if conditions allow, then to make a return breeding migration in August and September, nesting in the general area where dry-season concentrations occur. Sufficient information is not available to know whether itinerant breeding does, in fact, occur. However, opportunities seem to be available as nesting colonies have been found in the south from May to July (Kibish Hills 5°05′N × 35°37′E, Bor 6°15′N × 31°50′E) as well as in central Sudan during September and October, where enormous concentrations have been reported (Figs. 10.5, 10.6, and 10.7).

Very little is known about quelea movements in Sudan, such as the size and composition of groups and the distances and directions they travel. A single ringing recovery supports a movement between south-western Ethiopia and southern Sudan. An adult ringed in May 1980 at a nesting colony along the Kibish Hills (5°05′ N × 35°37′E) was recovered 260 km to the west at Kapoeta, Sudan (4°48′N × 33°35′E) on 26 July 1982. In May 1980, large numbers of quelea were reported moving south-east along the Akobo River (7°50′N × 33°00′E), a tributary of the Sobat River (Fig. 10.4), which forms the border with Ethiopia (T. Matonovich, pers. comm.). Possibly this was an early-rains migration to nesting areas along the lower Omo River (Fig. 10.4) in south-western Ethiopia. P. Ward (unpubl. data) has suggested an extra-seasonal movement of quelea to the Red Sea coast where December–January rains may allow nesting. In June 1979, Ward collected 6-month-old quelea near Khartoum (Lenton 1980), which he believed must have originated from either the Red Sea coast, or the southern flood zone in Jonglei Province, where grass growth can be months behind the rains when the flood waters recede. Evidence for winter breeding along the Red Sea coast of Sudan has not yet been found (J. Jackson, pers. comm.; G. Lenton, pers. comm.). Hailu (1984), however, found two nesting colonies near the Red Sea coast of Ethiopia along the lower Awash River (11°40′N × 41°30′E; Fig. 10.5) in March 1983. This was apparently due to to the unseasonally good rainfall in the previous January associated with the Red Sea Convergence Zone.

Ethiopia

Quelea movements within the Ethiopian Rift Valley were investigated from 1976 to 1982 (Bruggers *et al.* 1983; Erickson 1979; Jaeger *et al.* 1979, 1986). The main dry season (Oct.–May) concentration of adult quelea seemed to be in the north, particularly in the Awash River Basin (Fig. 10.4). Evidence from marking recapture, 'fingerprint' matching, and the pattern of disappearance and reappearance of quelea supports the migration model proposed by Ward (1971): an early-rains migration into the rainfront in May and June and a return breeding migration in August and September. Quelea disappear from the Awash Basin and nearby Lake Zwai (8°00′N × 38°53′E) in May and June, shortly after onset of the rains, coincident with the appearance of nesting colonies in south-western Ethiopia and adjoining Kenya (Fig. 10.5). 'Fingerprint' evidence also supports June–July nesting to the east of the Awash Basin in the northern Ogaden where the main rains begin in April and May. Quelea return to the Awash Valley in August and September where a second wave of nesting occurs. By November these colonies have dispersed, and quelea damage to ripening sorghum begins along the base of the highlands bordering the Awash Basin (Bruggers and Jaeger 1982; Jaeger and Erickson 1980). Quelea remain in the Awash Basin

until May–June when the cycle is repeated (see Jaeger *et al.* 1979 for sizes and locations of roosts).

Evidence for two successive breeding cycles by the same adults was obtained in the Ethiopian Rift (Jaeger *et al.* 1986). Quelea were mass-marked with aerially applied fluorescent particles in two separate nesting areas in south-western Ethiopia during June 1981. Marked adults from both areas were recovered up to 100 days later during August and September in nesting colonies in the Awash River Valley 500–700 km to the north of the spray sites. Nesting colonies in both the south-west and in the Awash Valley were scattered in time and space. Colonies in the Awash were distributed over more than 300 km of the valley, and were established over a 2-month period, which coincided with local differences in maturation of grasses. This wide distribution probably increases nesting success in areas of locally variable rainfall. This contrasts with a strategy of mass migration where concentrated breeding occurs where and when suitable conditions are first encountered (see Jaeger *et al.* 1986 for further explanation).

The recoveries of quelea ringed in Ethiopia between 1976 and 1982 (W. Erickson, unpubl. data) are presented in Table 10.1. One recovery further supports a seasonal movement from the southern Rift northward to the Awash River Basin (Ambo Pond to Lake Zwai). Eleven of thirteen recoveries are of adults ringed in the Awash Valley and recovered at the same or nearby sites, and in two instances at 33 and 35 months post-ringing. This suggests an affinity of quelea to familiar areas.

Somalia

Quelea in Somalia seem to be represented by two separate populations (Fig. 10.8*a*). Quelea in the north have similar mask indices to those from the nearby Awash River Basin of Ethiopia, while in the south they are similar to those from south-eastern Ethiopia and north-eastern Kenya. Ward (1971) believed that the quelea in southern Somalia had their major dry-season (June–Oct.) concentration in Tanzania. According to his model (Figs. 10.1, 10.2, and 10.3), with onset of the short rains in Tanzania in November, this concentration migrates to the north-east and into southern Somalia (Ward and Jones 1977) where the rains begin several weeks earlier and where nesting could begin. Ward (1971) believed that with favourable rainfall most quelea return to the south after a few weeks and nest in southern Kenya (Dec.–Jan.) and again in central Tanzania (Feb.–Mar.). From central Tanzania quelea turn back to the north and follow behind the passage of the long rains, nesting once or more often, and finishing this breeding migration in southern Somalia in June and July. Therefore, the same birds would have the potential to nest four or five times within a year.

Quelea movements and nesting in southern Somalia are now known to be

Table 10.1. Summary of recoveries of quelea ringed in Ethiopia (1977–1982).

Ringed				Recovered			
Location	Date	Sex	Age group	Location	Date	Distance (km)	Time (months)
Sodere[a] (8°25′ N × 39°25′ E)	12 May 77	M	Adult	Sodere[a]	11 July 77	0	2
Wonji[a] (8°30′ N × 39°15′ E)	21 May 77	Unknown	Adult	Nazareth[a] (8°35′ N × 39°15′ E)	22 Apr. 80	10	35
Melka Werer[a] (9°35′ N × 40°20′E)	10 June 77	M	Adult	Melka Werer[a]	29 Mar. 79	0	22
Sodere[a]	8 July 77	F	Adult	Lake Zwai[a] (8°05′ N × 39°00′ E)	4 Nov. 80	60	33
Tabila[a] (8°40′ N × 39°45′ E)	16 Sept. 77	Unknown	Adult	Melkassa[a]	18 Oct. 77	60	1
Melkassa[a] (8°25′ N × 39°20′ E)	13 Nov. 77	M	Adult	Melka Sadi[a] (9°25′ N × 40°20′ E)	17 Apr. 78	160	5
Melkassa[a]	13 Nov. 77	Unknown	Adult	Melkassa[a]	17 Jan. 78	0	2
Melkassa[a]	14 Nov. 77	Unknown	Adult	Melkassa[a]	18 Jan. 78	0	2
Melkassa[a]	14 Nov. 77	Unknown	Adult	Melkassa[a]	18 Jan. 78	0	2
Saluki[a] (8°40′ N × 39°25′ E)	11 Nove 77	Unknown	Adult	Saluki[a]	14 Jan. 78	0	2
Saluki[a]	11 Nov. 77	Unknown	Adult	Saluki[a]	14 Jan. 78	0	2
Kibish (5°05′ N × 35°37′ E)	28 May 80	M	Adult	Kapoeta, Sud (4°48′ N × 33°35′ E)	26 July 82	260	26
Ambo Pond (4°38′ N × 37°31′ E)	28 July 80	F	Juvenile	Lake Zwai[a]	28 Oct. 81	400	15

[a]Location is in, or in close proximity to, the Awash River Valley.

more complex than implied by Ward's model. First, quelea nesting in southern Somalia seems to be on a larger scale than that proposed by Ward (1971). Nesting has been found near the Juba and Webi Shebelli rivers (Figs. 10.4 and 10.5), where colonies are now regularly found in both May and June and November and December (Barré 1983; Bruggers 1980; Elliott 1980*a*). Nesting was also found along the Juba River in late August 1984 (M. Jaeger, pers. obs.), where M. Barré (pers. comm.) suggests that nesting at this time is a regular occurrence. Second, quelea nesting can occur simultaneously over a wide area (Figs. 10.1, 10.5, and 10.6). For instance, evidence of May–June nesting has been found in northern Tanzania, the southern Rift Valley of Kenya, south-eastern Kenya, southern Somalia, and south-eastern Ethiopia. Third, quelea have been found in southern Somalia during most of the year (Ash and Miskell 1983). Fourth, simultaneous collections have been made in southern Somalia where the 'fingerprints' do not match; for instance, quelea sampled at three different locations during the period July to September 1984 seem to be acting independently of one another (Table 10.2). 'Fingerprinting' analysis shows that quelea collected at Baidoa had not bred in 1984, while those from Jiohar bred in May–June, and those from Gilib in August–September. Furthermore, male mask indices differ between these samples ($P<0.001$) (Fig. 10.8*b*). Such a pattern of discrete variation in 'fingerprints' would seem to suggest separate movements between and cohesion within groups of quelea.

Table 10.2. 'Fingerprint' collections from southern Somalia during 1984.

Location[a]	Date collected	Nesting period	Male mask index[b] 1 and 2 (%)
Gilib (0°30′ N × 42°30′ E)	Sept.	Aug.-Sept.	66 ($n=176$)
Jiohar (2°30′ N × 45°30′ E)	July	May-June	45 ($n=264$)
Baidoa (3°00′N × 43°30′ E)	July	No nesting	57 ($n=1334$)

[a] By 1/2° grid square.
[b] Chi-square = 20.3, $P<0.001$.

Kenya

Present evidence in Kenya supports two distinct populations (Figs. 10.8*a* and 10.8*b*), one across southern and eastern Kenya associated with southern Somalia and Tanzania, and the other from the central to northern Rift Valley connecting with quelea in the Ethiopian Rift Valley; however, nothing is known about quelea movements and their affiliations in north-eastern Kenya. Nesting occurs in south-eastern Kenya in May–June, August–

September, and December–January (Allan 1983; J. Thompson and M. Jaeger, unpubl. data), similar to southern Somalia. From December 1984 to May 1985, a period of exceptionally good and prolonged rains, nesting colonies were found in Tsavo East National Park, where evidence was found of two nestings in succession by the same birds. Likewise, in this area first-year quelea hatched in May–June or August–September 1984 seemed to be breeding. It seems, therefore, that in years of favourable rainfall, quelea can remain in eastern Kenya throughout most of the year, and that this general area can be an important regional focus for reproduction.

Recoveries of quelea marked with fluorescent particles support some movement between Tanzania, eastern Kenya, and southern Somalia following the general direction of movement proposed by Ward (1971) and Ward and Jones (1977). A single adult male quelea marked on 15 June 1984 at a nesting colony on the Tanzania-Kenya border near Taveta, Kenya (3°30′S × 38°00′E),* was recovered on 28 September 1984 at a roost 450 km to the north-east on the Kenya–Somalia border near Kiunga, Kenya (1°30′S × 41°00′E). Similarly, two adult females marked at nesting colonies in the Tsavo East National Park of eastern Kenya on 19 January (2°30′S × 38°00′E) and 2 March (3°00′S × 39°00′E) 1985, respectively, were recovered from a nesting colony on 29 March 1985, 460 km to the south-west near Dodoma, Tanzania (5°30′S × 35°00′E). Meanwhile, other quelea remained in and around the Tsavo East National Park, where nesting continued until June 1985. This further indicated a fragmented nature of quelea movements in the region.

In Kenya, quelea are also found in the Rift Valley, where they are an occasional pest of ripening wheat and barley grown along the highlands forming the Rift (Allan 1983; Williams 1954). Surveys have focused in the southern portion of the Kenyan Rift, where nesting is commonly found during May and June along the Tanzanian border near Lakes Natron and Magadi (Fig. 10.4; Kitonyo 1981, 1983). It has been suggested that these quelea attack wheat to the north near Ngorengore (1°00′S × 35°30′E) in May/June and Nakuru (0°00′S × 36°00′E) during July/August. Quelea collected at Ngorengore during August 1984 had a 'fingerprint' matching that of quelea nesting in northern Tanzania during May and June 1984 and supporting a northward movement into Kenya. Quelea collected further to the north near Nanuyuki (0°00′N × 37°00′E) in June and at Nakuru in July 1984 had similar 'fingerprints,' but differed from those from Ngorengore and Tanzania. The available evidence (Figs. 10.8*a* and 10.8*b*) suggests that the quelea found in the central Rift of Kenya are more closely aligned with quelea from northern Kenya and south-western Ethiopia, in agreement with Williams (1954). There is also a possible connection with southern Sudan and eastern Uganda.

*This coordinate and all subsequent coordinates represent 1/2° grid squares.

Quelea are not commonly reported from western Kenya, except to the south near Kisumu (0°00′S × 34°30′E) on Lake Victoria where a collection was made in August 1984. The 'fingerprint' was similar to that from Ngorengore, 1984, with evidence of recently completed nesting since May and an earlier nesting during March, probably in central Tanzania. In April/May 1986, quelea were found breeding in sugar-cane near Kisumu, but no mask index data were collected (J. Gatimu, pers. obs.).

Tanzania

The gradual northward movements of quelea from breeding in central and southern Tanzania in February/March to breeding again in May/June is long established (Disney and Haylock 1956). Migration through Tanzania is fragmented and is probably spread across a wide front including western Tanzania, from where little information is available. It is not clear what occurs following the May/June nesting, and when or by what routes quelea return to breed the following spring. There may be an exodus of adults in June that has been masked by the presence in northern Tanzania of a substantial population of juveniles and some adults. If such an exodus occurs, it could involve a movement of birds across Kenya into southern Somalia where breeding occurs in June/July. The only evidence for this is the single recovery of an adult marked in June at a nesting colony on the Kenya-Tanzania border near Taveta, Kenya, and recovered in late September on the Kenya–Somalia border near Kiunga, Kenya. Many quelea probably remain in northern Tanzania through the dry season from June to October (Disney and Haylock 1956; Ward 1971).

There are two theories for the movement which occurs with the onset of the short rains in November. One is that the quelea move north-east into southern Kenya, where some nesting could occur during December and January before the birds move back to southern Tanzania in February and March to start a new breeding cycle (Disney and Haylock 1956). In support of this, quelea ringed at nesting colonies in central and northern Tanzania were recovered to the north and north-west in the Kenyan Rift and Lake Victoria area (Disney 1960). Support is also provided by the 1984 'fingerprinting' described above for Kenya, and the theory in general is consistent with the evidence collected in Tanzania since 1979 (Figs. 10.6 and 10.7).

The second theory is that with the onset of the short rains, quelea depart north-eastern Tanzania for southern Somalia, whence they initiate a south-westward wave of breeding back to central and south-western Tanzania by March (Figs. 10.1, 10.2, and 10.3; Ward 1971). Ward's evidence is weak, being a failure to locate quelea anywhere in Kenya or Tanzania in any numbers in late November and early December in 1969, and a single observation of southward-flying flocks in eastern Kenya in December. Given

the vastness of the area, it would be easy to miss quelea concentrations. Subsequent work by FAO projects has shown that breeding regularly occurs in southern Somalia in November/December, but no connection between this and the Tanzania population has been established other than that the mean mask indices for the two areas are similar. The evidence suggests that shorter, overlapping migrations may be occurring along this route, as implied in earlier discussions on quelea movements in southern Somalia and eastern Kenya (Fig. 10.7). The timing and routes of these migrations, together with the occurrence of nesting, are probably subject to considerable year-to-year variation depending on the pattern of rainfall.

Present evidence also tends to refute a southward wave of breeding through Tanzania from December to February following the short rains as proposed by Ward (1971). First, nesting colonies have rarely been found in northern Tanzania during this time. Second, the 'fingerprints' from collections made at nesting colonies in central Tanzania during February and March suggest that these birds have not bred within the previous 6 months (Luder and Elliott 1984). The nature of the southward movement of quelea back to south-western and central Tanzania is unknown.

Quelea movements in Tanzania may be further complicated by a regular influx of quelea from northern Zambia and/or western Tanzania (Ward 1966, 1971; Figs. 10.1, 10.5, and 10.8*a*). For instance, extensive nesting by quelea was reported in the Ruhkwa Valley of south-western Tanzania (Fig. 10.4) from March to May 1956 (Vesey-FitzGerald 1958). This implies an influx of quelea from the Rift Valley of western Tanzania, Burundi, Rwanda, and western Uganda. Unfortunately, very little is known about the quelea from this area.

Group cohesion

Group cohesion may be another important characteristic of quelea movements in addition to their being fragmented and changeable depending on the rainfall pattern. There seems to be a tendency for the same birds to remain together when migrating or when otherwise moving from one roosting area to another. This is of potential importance to a strategy of selective control, if it allows the prediction of where quelea that damage cereals come from. Evidence for group cohesion was mentioned earlier in regard to the variation between 'fingerprints' from three different localities in southern Somalia in 1984. In addition, the grouped pattern of recoveries of ringed or fluorescent masked quelea supports group cohesion (Jaeger *et al.* 1986). For example, from one marking site in Kenya in 1984, all 36 recoveries were made in the same area, 100 km away and up to 128 days post-marking. In another instance, an estimated 900 000 adults and 2 million juveniles were marked in four neighbouring nesting colonies near Makuyuni, Tanzania,

during June 1984. By early July, all of these colonies were deserted and quelea seemed to have departed the area. Subsequent collections from 11 sites in Tanzania ($n=3966$ birds), 6 sites across Kenya ($n=3131$ birds), and 3 sites in southern Somalia ($n=1493$ birds) between July and October failed to find a single marked bird. One explanation is that the sampling was not sufficiently widespread and that the marked birds remained grouped and were missed.

Implications for control

Much remains to be learned about the seasonal distribution and movements of quelea in eastern Africa as they relate to cereal damage. What we do understand about these movements suggests that the regional picture is complex. The following findings support this complexity:

(1) Quelea are widely distributed within the region.
(2) Based on the composition of male mask types, three or more populations are present with widespread intermixing among them.
(3) Nesting is widely scattered in time and space.
(4) Multiple nesting by the same birds can occur within a year.
(5) Migrations within a population are fragmented in time and space.
(6) Quelea may be long-distance migrants in some situations and have much shorter movements in others.

This complexity suggests a more localized approach to studying quelea distribution and movements as opposed to a regional population approach. Susceptible cereals, such as dryland sorghum and millet, are not uniformly distributed within the region, but rather are concentrated in areas such as the Singida region of Tanzania, the Gedaref area of Sudan, the Awash Basin of Ethiopia, and the Hargeisa area of northern Somalia. It is relative to those areas that quelea movements and distribution should be studied. The resulting information would allow determination of the most effective control strategy for local conditions. In some cases, it would be better to destroy nesting colonies before they disperse to cereal areas (Jaeger and Erickson 1980), while in other cases it would be more effective to leave them and wait to destroy the roosts that may develop in close proximity to cropping areas (Elliott 1983*a*). Selective control based on understanding the major concentrations of susceptible cereals and quelea movements in relation to them, proved to be effective in Ethiopia (Bruggers and Jaeger 1982; Jaeger and Erickson 1980).

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