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Evidence of itinerant breeding of the Red-billed Quelea *Quelea quelea* in the Ethiopian Rift Valley

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This paper provides evidence for itinerant breeding by Red-billed Quelea *Quelea quelea* in the Ethiopian Rift Valley. Queleas were mass-marked with aerially applied fluorescent particles in two separate nesting areas in southwestern Ethiopia during June 1981. Marked adults from both areas were recovered from nesting colonies in the Awash River Valley during August and September, up to 100 days post-spray and between 500 and 700 km to the north of the spray sites. In the Awash colonies, the presence of marked adults in breeding plumage with interrupted primary wing-moult, together with two age classes of juveniles, suggests that this was the second nesting. The progress of both the post-breeding and post-juvenal primary moults was consistent with an earlier breeding in May and June. The timing of the arrival and departure of birds from these nesting areas also supported the occurrence of double breeding by the same birds. Furthermore, the composition of black facial mask types of adult males was more similar between samples from the southern Ethiopian Rift and Awash Valley than between samples from either of these areas and samples from outside the Rift, providing additional evidence that the same population of birds bred in these two areas of the Rift Valley.

Nesting colonies in both areas were scattered in time and space. Colonies in the Awash were distributed for more than 300 km and were established over a two-month period, which coincided with local differences in the timing of the seeding in grasses. This wide distribution probably increases nesting success in such areas of locally variable rainfall. This contrasts with a stategy of mass migration, where concentrated breeding occurs where and when suitable conditions are first encountered.

Knowledge of the location and timing of previously successful nesting areas may increase the success of itinerant breeding, as Queleas seem to use the same areas in successive years if conditions are favourable. Recoveries of marked birds in the Awash were segregated according to both spray site and sex, suggesting some degree of group cohesion by sex from the first to the second nesting. We speculate that post-nesting group cohesion of adults may provide a means to maintain the integrity of collective group information on seasonal movements. Group cohesion may be facilitated by the high degree of nesting synchrony within colonies.

It has been speculated that Red-billed Quelea were multibrooded in some parts of their range in Africa, although perhaps not at the same locality (Williams 1954, Disney & Marshall 1956, Morel & Bourlière 1956, Ward 1965a, 1971). Ward (1971) suggested that nesting could occur two or more times following the path of the seasonal rainfront, and successive colonies could be hundreds of kilometres apart depending on the speed of movement of the rainfront and the distribution and timing of seeding grasses. He suggested that this 'itinerant breeding' was an adaptation to a locally short-lived food supply, and was possibly a strategy used by other birds of the

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semi-arid tropics. Itinerant breeding has subsequently been suggested for the Eared Dove *Zenaida auriculata* in association with the geographical movement of the rainy season in semi-arid Brazil (Bucher 1982). However, in neither situation has conclusive evidence for itinerant breeding been presented.

Queleas had previously been found nesting in southwestern Ethiopia during May and June 1979 and 1980, and 500 to 700 km to the northeast in the Awash River Valley from mid-August to October 1978, 1979, and 1980 (Jaeger *et al.* 1979, Jaeger & Erickson 1980, Bruggers & Jaeger 1982). Previous evidence based on timing of seasonal rains in relation to the presence of Queleas in both areas; interrupted primary wing-moult (Harper 1984) in Awash colony adults; two- to three-month-old juveniles collected in association with the Awash colonies; and similarity in the shape of the facial mask of males from both areas suggested that the same birds could be breeding in both areas. Our objective in this study was to determine whether Queleas, marked in breeding colonies in southwestern Ethiopia, did indeed move north to the Awash River Valley and breed a second time. In no part of its range had the seasonal distribution and movement pattern of a Quelea population been determined, primarily due to the difficulty in locating Quelea nesting colonies in the more remote areas and to the lack of a practical means of marking birds in these aggregations. Distribution and movements of Queleas in the Ethiopian Rift Valley are discussed in relation to nesting strategy.

Study area and methods

Fieldwork was conducted from April to November 1981 in the Ethiopian Rift Valley and adjoining areas of Kenya and Somalia (Figs. 1 & 2), where both elevation and seasonal rainfall are important determinants of Quelea distribution. The Rift divides the major highland regions of Ethiopia by a lowland corridor extending from the semi-arid grasslands of the southwest to those of the Awash River Valley and Jijiga Plain to the northeast. These plateaux restrict the movement of Queleas, which are rarely found above 1800 m (Urban & Brown 1971, Jaeger & Erickson 1980). Nesting commences six to eight weeks after the onset of the seasonal rains (Ward 1971).

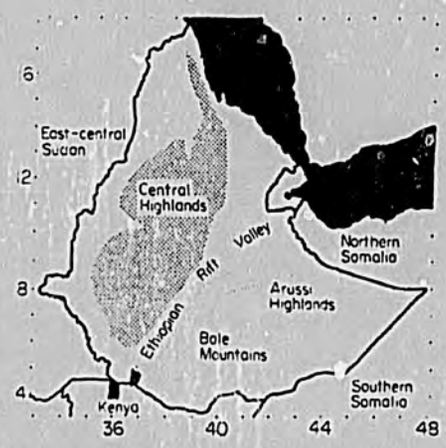

Figure 1. Map of Ethiopia illustrating the Ethiopian Rift Valley and the general area over which surveys were undertaken during 1981.

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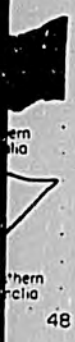

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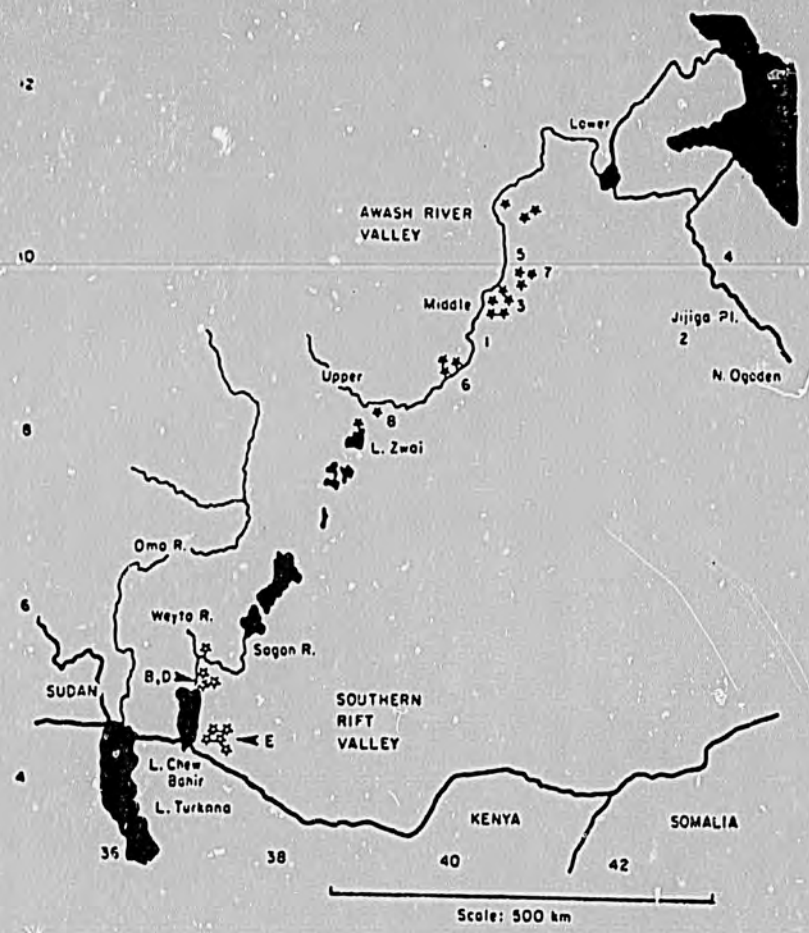

Figure 2. Distribution of Quelea nesting colonies and sampling sites in the Ethiopian Rift Valley and northern Ogaden during 1981. Nesting Sites ☆ May–June; ★ August–September.

which begin in the southern Rift in March and move northward to the Awash Valley by July. For a description of the movement of the Intertropical Convergence Zone (ITCZ) that is responsible for the onset of the rainy season see Brown *et al.* (1982).

Nesting colonies were located by helicopter and by radio-tracking Queleas equipped with miniature transmitters (Bruggers *et al.* 1983). Surveys focused in the 1200 km^2 basin of Lake Chew Bahir, which is drained by the Weyto River (Fig. 2), and on the plains to the southeast which lie near the Kenya border. Three nesting colonies (B, D and E; Fig. 2), ranging from 8 to 14 ha were marked with Day-Glo^{R*} fluorescent particles between 15 and 17 June. Colonies B and D, located north of Lake Chew Bahir in the Weyto River delta, were aerially sprayed with red fluorescent particles (Johns *et al.*, in prep.). Colony E, approximately 80 km to the southeast, was sprayed with yellow fluorescent particles. Spraying took place just after sunset when the adults were concentrated within the colonies.

Following spraying Queleas were mist-netted at three separate sites within each colony to estimate the numbers marked. Plumage was inspected for fluorescent markers in the dark using ultraviolet light. The percentage marked was multiplied by

* Reference to trade names does not imply U.S. Government endorsement.

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the estimated number of birds in each colony, as determined by sampling the number of occupied nests along transects as described by Elliott (1981). From July to October, birds were collected in the Rift to the northeast of the marking sites and examined for marked birds (Fig. 2). The entire Awash River Valley, a distance of about 560 km, was surveyed by air and ground teams. Constraints of time and personnel did not allow for surveys or collections in other directions away from the marking sites.

Birds from nesting colonies in both the southern Rift and Awash Valley were examined for evidence of previous breeding, such as adults with interrupted moult (see Ginn & Melville 1983 and Harper 1984 for moult terminology) and older juveniles. The progress of primary wing-moult was quantified by scoring individual primaries of the right wing, from inside to out, using the 0–5 point system (after Sealy 1979). A score of 0 indicates that the moult has not yet begun, and a score of 45 that it was completed. With interrupted moult new feathers are fully grown, but distinguishable from the old feathers by lack of wear and fading.

Juveniles can be approximately aged by the progress of the post-juvenal moult. Post-juvenal moult of the primaries begins at about 11 weeks post-hatching and is completed in approximately four months, or six to seven months post-hatching (Morel & Bourlière 1955, Ward 1973, Elliott, unpublished). Adults were distinguished from juveniles using a combination of the 0–4 cranial pneumatization index of Ward (1973), together with bill colour and plumages characteristic of each group. Birds with cranial pneumatization of 2–4 were considered adult. Birds with cranial pneumatization of 0 or 1 were considered juveniles, unless completion of post-juvenal moult indicated otherwise. Nesting colonies were aged using the schedule of Ward (1973).

Quelea populations are polytypic for the extent of the black face mask of adult males (Ward 1966, 1973). Males in breeding plumage were collected from nesting colonies in both the southern Rift and Awash Valley for comparison with samples from Sudan and Somalia. The extent of black in the frontal band was scored from 1 to 7 (Ward 1973) where 1 represents the absence of a frontal band and 7 a broad band. Mask types 1 and 2 were grouped for analysis as they are sometimes difficult to distinguish.

Results

Southern Rift Valley

Nesting colonies

Nine nesting colonies were found in the southern Rift of Ethiopia (Fig. 2) and an additional 14 in adjoining northern Kenya (Allan, pers. comm.). Other colonies probably occurred as this was not an exhaustive survey. Most colonies were established between mid-May and early June, and the breeding cycle was completed by mid-July. One small colony, however, was found to have been established in late April and was successfully completed by 2 June. Only a single colony was known to have been abandoned prior to completion of nesting. No concentrations of Queleas were found in the southern Rift Valley of Ethiopia until just before nesting commenced, suggesting a rains-related immigration (called an 'early-rains migration' by Ward 1971).

Queleas collected along the lower Omo River on 20 May ($n = 111$) and from Colonies B and D from 17 May to 3 June ($n = 409$) showed no evidence of prior

Table 1. *Estimated number of Red-billed Quelea marked with fluorescent particles in southwestern Ethiopia*

Spray target	Coordinates	Colour	Samples: Adults *n*	Adults % marked	Fledglings *n*	Fledglings % marked	Estimated no marked: Adults	Fledglings
Colony B*	5 01'N. × 36 57'E.	Red	273	42	335	82	195 000	459 000
Colony D†	4 59'N. × 36 58'E.	Red	372	51	·	·	115 000	...
Colony E*	4 30'N. × 37 00'E.	Yellow	40	3	693	47	20 000	443 000
							330 000	902 000

* Fledgling stage; † nestling stage.

breeding. Only six individuals from these samples had cranial pneumatization scores of 0 or 1 and were undergoing post-juvenal moult of the primaries. However, their moult scores ranged from 42 to 44, suggesting that they were at least six months old. None of the adults was moulting primaries or seemed to have interrupted wing-moult.

Mass-marking

An estimated 1·2 million Queleas (0·3 million adults and 0·9 million fledglings) were marked with fluorescent particles (Table 1). Ninety-four per cent of the adults were from Colonies B and D and were red-marked. Three per cent of 40 adults collected near a waterhole by Colony E were marked with yellow particles. However, birds from other unmarked nearby colonies intermixed at this location. The estimate of marked fledglings was equally divided between the red and yellow. In general, adults

Table 2. *Progress of the primary feather moult of Queleas collected in the Awash River Valley and adjoining areas of the northern Ogaden during July–September 1981*

Location	Map site (Fig. 2)	Collection: Date	Collection: Site*	Primary feather moult (*n*): Juveniles: Pre-moult	Juveniles: Active†	Juveniles: Inter-rupted	Adults: Pre-moult	Adults: Active†	Adults: Inter-rupted	Adults: Post-moult‡
Melka Sede	1	24 July	Roost	7	9	—	52	21	—	—
Fafam	2	1 Aug	Roost	81	2	—	111	76	11	—
Issa Plain	3	7 Sep	Colony	10	3	2	418	21	374	(418)
Gewane I	5	12 Sep	Colony	38	38	19	7	1	18	(7)
Gabile	4	15 Sep	Roost	26	3	2	4	15	39	—
Gewane II	7	16 Sep	Colony	6	—	2	29	—	30	(29)
Nura Hera	6	17 Sep	Colony	7	—	1	68	—	28	(68)
				175	55	26	689	134	500	(522)

* 'Roost' = aggregation of non-breeding birds; 'Colony' = aggregation of breeding birds.

† Active moult was not distinguished from interrupted moult where the feather at the point of interruption was still growing.

‡ Parentheses indicate that post-moult feathers could not be reliably distinguished from pre-moult feathers.

seemed to be better marked than juveniles, particularly on the wings—probably the result of their flying up through the spray - whereas fledglings remained within the thornbush.

Awash River Valley

Nesting colonies

Sixteen nesting colonies were found in the Awash Valley and at nearby Lake Zwai during September 1981 (Fig. 2). An additional colony probably occurred along the western shore of Lake Zwai. Colonies in the middle Awash Valley were established from early August, while those in the upper Awash Valley and Lake Zwai were established from mid-September. This was consistent with the past distribution and timing of nesting in the Awash Valley (Jaeger *et al.* 1979, Jaeger & Erickson 1980). Large concentrations of Queleas are generally found in the Awash Valley during the dry season (October to May), but are absent from mid-May to mid-July, disappearing shortly after the onset of the rains (Jaeger *et al.* 1979).

Interrupted primary moult and the presence of an age class of older juveniles suggested that this was the second nesting for many of the adults in the Awash Valley colonies. Queleas were collected from seven widely-scattered sites from 24 July to 17 September (Table 2). These included three night roosts and four nesting colonies. Of the 1323 adults examined, 48% were either moulting the primaries ($n = 134$) or had interrupted the moult ($n = 500$). Interrupted moult was more common in adults collected in nesting colonies (95% of 472 moulting birds) than in adults collected from roosts (31% of 162 moulting birds). Juveniles from an earlier nesting also were found in these samples. At the Gewane I nesting colony (Site 5, Table 2; Fig. 2), 60% of the 95 juveniles collected had begun the post-juvenal primary moult, indicating that these birds were approximately three months old and, therefore, hatched in May or June, consistent with a southern Rift origin.

Recovery of marked Queleas

A total of 3197 Queleas was collected and examined for markers from eight sample sites between 24 July and 25 September (Table 3; Fig. 2). Thirteen marked Queleas,

Table 3. *Description of recoveries of fluorescent-marked Queleas from sampling sites associated with the Awash Valley*

Map site (Fig. 2)	Date	Type	Age (days)	Sampled *n*		Recovered *n*				Distance travelled (km)	Time elapsed (days)
						Yellow		Red			
				Juvenile	Adult	Male	Female	Male	Female		
1	24 July	Roost	—	15	74	2	0	0	0	650	67
2	1 Aug	Roost	—	93	189	0	0	0	0	—	—
3	7 Sep	Colony	17	0	1000	0	1	0	0	650	86
4	15 Sep	Roost	—	230	66	0	0	0	0	—	—
5	17 Sep	Colony	40	0	200	0	0	6	0	700	93
6	17 Sep	Colony	25	0	800	0	0	0	0	—	—
7	18 Sep	Colony	40	0	50	0	0	1	0	700	94
8	25 Sep	Colony	3	0	480	0	3	0	0	500	100
				338	2859	2	4	7	0		

seven red and six yellow, were recovered from five of these sites. All markers were on old and worn primaries. Eleven of the recoveries were from four nesting colonies between 500 and 700 km away from the colonies in which they were marked. The remaining two were found in a roost in the middle Awash prior to the establishment of the first nesting colonies. The recoveries comprised 12 adults (eight males and four females) and one apparent juvenile male. The interval between marking and recovery ranged from 67 to 100 days. No colonies or roosts were found between the southern Rift and Lake Zwai, suggesting that birds migrated directly through this corridor without stopping.

Five of the marked Queleas (three males and two females) had interrupted moult at one of the first three primaries. One female was actively moulting the fourth primary. Six adults had not yet begun the primary wing-moult. All of the above were in breeding plumage and had cranial pneumatization scores of 4. Gonads could not be measured due to spoilage. The remaining marked Quelea was a male in breeding plumage with a cranial score of 1 and primary moult score of 0, suggesting a juvenile less than 11 weeks old. (See Ward 1971 for a discussion of juveniles moulting directly into breeding plumage.)

Marked Queleas arrived in the Awash Valley in separate groups during a two-month period and were segregated by origin (red *vs.* yellow fluorescent markers) and sex. The earliest recoveries were two yellow-marked males from a small night roost in the middle Awash on 24 July (Site 1, Table 3; Fig. 2). Seven red-marked males were later found in two adjacent nesting colonies (established in early August) in the middle Awash (Sites 5 and 7). A single yellow-marked female was recovered from a nearby colony (Site 3) established in late August. Finally, three yellow-marked females were found in a newly-established colony (Site 8) in the upper Awash on 25 September, where Queleas had not been seen during the previous three months. It is unlikely that these birds came from recently-completed colonies in the middle Awash (Sites 5 and 7) as these colonies appeared to have been effectively destroyed by control operations. (See Jaeger & Erickson 1980 and Bruggers & Jaeger 1982 for description of Quelea control in the Awash Valley.)

A separate ringing recovery further supported a northward migration from the marking sites. An adult female that had been ringed in the southern Rift near the site of Colony E on 25 July 1980, together with 3000 other juveniles, was recovered at Lake Zwai, 400 km north of the ringing site, on 28 October 1981. This female had a cranial score of 4 and interrupted moult at primary six. Another ringing recovery, however, suggested that Queleas nesting to the west along the lower Omo River may subsequently move west into the Sudan. An adult ringed in late May 1980 at a nesting colony on the Sudan border (5°05′N × 35°37′E) was recovered 260 km to the west at Kapoeta, Sudan on 26 July 1982.

Table 4. *Comparison of male mask types of Queleas in the Ethiopian Rift Valley with those from adjacent Sudan and Somalia*

Gradient	Region	Sample sites *n*	Years sampled	*n*	% mask types 1 and 2*
Northwest	East-central Sudan	4	1979–81	895	97
Ethiopian Rift	Awash River Basin	5	1981	1 609	85
	Southern Rift	5	1981	2 283	80
Southeast	Southern Somalia	4	1979–81	1 467	67

* Mask types 1 and 2 have little or no frontal band.

Male facial mask

A gradient occurs in the frequencies of Quelea mask types across Ethiopia from southeast to northwest, with the highest proportion of queleas with frontal bands (scores 3–7) being found in southern Somalia, and the lowest proportion being found in east-central Sudan (Table 4). Mask indices scores of birds collected within the Rift were intermediate and closer to one another than to those of birds collected in Somalia or Sudan. However, samples from the southern Rift and Awash differed significantly from one another in the overlap of Bonferroni confidence intervals (Miller 1966) for the combined proportion of mask types 1 and 2 ($P < 0.05$). This suggests some intermixing from outside the Rift.

Discussion

Evidence in support of itinerant breeding

The recapture of marked Queleas at nesting colonies in the Awash Valley provides strong evidence for itinerant breeding in birds. This is supported by the occurrence in these colonies of a high percentage of adults with interrupted primary wing-moult and a second, older age class of juveniles. Furthermore, the seasonal distribution of Queleas in the Rift and the timing of nesting followed the movement of the rainfront and seeding of grasses as predicted by Ward (1965a,b, 1971).

Our marking results do not allow us to determine the number of Queleas that moved from the southern Rift into the Awash Valley. Only a small percentage of Queleas in the southern Rift was marked, these being from only three of the 23 known colonies. In addition, the Awash samples may represent a mix of adults originating from both the southern Rift and the northern Ogaden, where the annual occurrence of large concentrations of juveniles suggests a June nesting in the area. Furthermore, it is likely that many marks were lost through feather wear and moult.

In addition to the recovery of marked Queleas, two lines of evidence support a general movement from nesting areas in the south, northward into the Awash Valley. Firstly, adults leave the southern Rift study areas following nesting. In late July 1979, five recently-abandoned Quelea colonies were found in the same area in which Colonies B and D occurred in 1981. Most adults seemed to have departed from the general area. However, two concentrations remained, one predominantly male and the other female. The males had large fat deposits suggesting impending migration (Ward & Jones 1977, Jaeger *et al.* 1979), whereas females did not and appeared in poor condition. Similarly in 1980, adults departed from nesting colonies near Colony E by late July, leaving behind an enormous concentration of juveniles. This departure from the south coincided with the reappearance of Queleas in the Awash Valley. In 1981, this reappearance was first observed on 24 July. Secondly, the similarity in composition of male mask types between samples from south and north further supported movement and intermixing within the Rift.

Despite the preceding evidence, it cannot be determined if the recaptured Queleas were successful in both nesting attempts. However, non-breeding or reproductively asynchronous adults did not appear to remain in nesting colonies beyond the initial few days of colony formation (Bruggers & Jaeger, in prep.). Likewise, the occurrence of interrupted primary wing-moult in the marked recoveries from colonies indicated that double breeding was at least attempted; and breeding was successful in both the marked colonies and those from which recoveries were made. It is likely that non-breeding Queleas did not moult in synchrony with

the breeding birds, and that interrupted moult in the Awash colonies was a response to breeding and not to migration.

Time interval to renesting

Ward (1971) suggested itinerant breeding to be an uninterrupted succession of nesting, where the adults abandon a completed colony and move on, following the path of the rainfront, to renest within only a few days. Ward's (1971) evidence was his finding a nesting colony in northern Tanzania in its final days, in which some adult females had nearly fully-grown ova and were apparently ready to renest. However, subsequent evidence suggested that following breeding, the nutritional state of Queleas is often below peak condition necessitating time to replenish reserves (Jones & Ward 1976, Fig. 13).

In our study, where nesting followed the northward movement of the ITCZ, there was an interval of one to three months between the end of the first nesting and start of the second. The patchy distributions of suitable nesting habitat in the Rift probably prohibits renesting to the north before mid-August in the middle Awash. This pattern of rainfall and nesting in the Ethiopian Rift seems to be the usual pattern and not unique to 1981.

A comparable one- to three-months interval before renesting has been observed elsewhere in Africa. In Tanzania, for instance, the opportunity for immediate renesting (i.e., suitable habitat) seems to exist, because a succession of nesting colonies has been recorded along the south to north axis from February to June with the northward movement of the rains (Elliott, pers. comm.). However, nesting occurs in two major peaks, the first during February and March in the south and the second during May and June in the north (Disney & Haylock 1956, Luder & Elliott, unpublished). As in our study, the later colonies usually contain a high percentage of adults with interrupted primary wing-moult, together with a second, older age class of juveniles, approximately 12 weeks old; the frequencies of male mask types are consistent with those from the south. The longer time interval may be needed to prepare physiologically for re-nesting, particularly if it is to be preceded by a long migration (Ward & Jones 1977).

'Itinerancy' implies a geographical separation in breeding attempts following movement of the rainfront. However, examples exist of multiple breeding within a year which do not seem to fit this definition. A bi-seasonal pattern of multiple breeding can occur in the same area where there are two or more distinct and regular seasons of rainfall such as occur in southern Somalia, where nesting has been recorded from May to September and in December and January (Bruggers 1980, J. S. Ash, pers. comm.). Opportunistic breeding can also occur in response to an unseasonal good rainfall, as was apparently the case in the lower Awash Valley where two nesting colonies were found during March 1983 (Hailu K., pers. comm.). Here the January rainfall associated with the Red Sea Convergence Zone is normally less than 50 mm and generally insufficient for Quelea nesting. Evidence of double breeding in the same general area during a prolonged period of rains was found in southeastern Kenya in 1984 and 1985. Nesting occurred from November to May in or bordering Tsavo East National Park (Thompson & Jaeger, in prep.). Two adult females (with brood patches), which had been marked with fluorescent particles 6 weeks earlier in a colony 125 km away, were recovered in late March from another nesting colony.

Fragmented migration

Seasonal movements of Queleas have been described as nomadic (Disney & Marshall

1956, Brown *et al.* 1982), migratory (Ward 1971, Ward & Jones 1977) or a combination of the two (Lack 1966). Fat deposition, induced by the onset of the seasonal rains and occurring before departure from dry-season concentrations, suggests migration (Ward & Jones 1977). The pattern of disappearance and reappearance of Queleas in the Ethiopian Rift supports the migration model proposed by Ward (1971): an 'early-rains migration' into the rainfront, and the return 'breeding migration' following behind the rainfront (see Endler 1977, p. 21, for characteristics defining migration). Migration routes, however, are probably susceptible to interruption or alteration as a consequence of major irregularities of rainfall, particularly drought.

In our study, the two-month period over which marked Queleas arrived in the Awash Valley and established nesting colonies implies a fragmented migration from the southern Rift as opposed to a single mass migration. Reappearance coincided with the local availability of ripening grasses which seed first in the middle Awash and later in the upper Awash Valley. The segregated distribution of marked recoveries in the Awash further supports a fragmented migration. Yellow- and red-marked Queleas were not found together in any of the recovery sites, implying that intermixing had not taken place, and that birds from the two separate areas had moved independently. This segregation is probably the result of both the distance between the marked colonies and a difference in the date of completion and abandonment by the adults of the two areas.

Marked birds that were recovered were segregated sexually by collecting site, suggesting that adult males and females migrated separately. Sexual segregation in adult Queleas is commonly observed in nesting colonies before abandonment by the adults (Disney & Haylock 1956, Allan & Jackson, unpublished, Jaeger, pers. obs.) and between roosts prior to the early-rains migration (Jaeger *et al.* 1979). Differential timing in migration between the sexes may result from physiological or behavioural differences in preparedness to migrate. This is consistent with previously mentioned findings from Lake Chew Bahir where, in late July 1979, one sample of 700 post-breeding Queleas was 94% male, and a second sample of 450 birds from 25 km away was 74% female. The males had abundant fat, while the females appeared to be in relatively poor condition with no visible fat, suggesting that the males would migrate first. Post-breeding segregation of adults and juveniles also occurs. Many juveniles often remain in the general area of the colony for several weeks after adults leave (Crook 1960, Ward 1971, Jaeger *et al.* 1979), and this segregation may be maintained throughout the juvenile period (Jaeger *et al.* 1979). In our study, some juveniles migrated north with the adults.

Traditional nesting areas

Nesting occurs over large tracts of the Ethiopian Rift, but it seems to be concentrated in traditional areas. In 1981, for example, the four colonies located at Lake Chew Bahir in the southern Rift were within a 15-km radius of one another, three being within a radius of 1 km. Five nesting colonies are known to have occurred in the same area in 1979, and at least two in 1982. In 1981, multiple-colony groups were also found in two other areas of the southern Rift and in four areas of the middle Awash Valley; with one exception, all areas were known to have had nesting colonies in previous years. In addition, Queleas traditionally nest in the lower Omo River Valley and at Lake Zwai and Malkassa (Site 8, Fig. 2) in the upper Awash Valley, where multiple colony groups have been found in the past. It is not uncommon in these areas for nesting to be in the same trees in successive years, as has been observed elsewhere (Disney & Haylock 1956, Luder, pers. comm.).

The formation of one multiple-colony group was followed in 1981 in the southern Rift by radio-tracking Queleas (Bruggers *et al.* 1983, Bruggers & Jaeger in prep.). Here, three colonies formed successively over a two-week period from a single asynchronous aggregation, which sorted itself into colonies based on reproductive synchrony. The result was synchrony within, but not among, colonies in the same area. A similar pattern of successive colony formation was found in mixed colonies of Black-headed Weavers *Ploceus cucullatus* and Masked Weavers *P. intermedius* in southern Ethiopia (Bruggers *et al.*, 1985). Successive colony formation is consistent with observations on Queleas elsewhere in the Ethiopian Rift, and it offers an explanation for the great variability in colony size (Disney & Haylock 1956, Morel *et al.* 1957, Vesey-Fitzgerald 1958, Ward 1965a). For example, successful colonies found in Ethiopia have ranged in size from less than 0·25 ha to greater than 70 ha, and from a few thousand nests to nearly a million (Erickson, in prep.).

Asynchrony among nearby colonies, together with great variability in colony size, seems to weaken most arguments expounding the advantages of synchrony within colonies namely swamping predators (Lack 1968) and information transfer about locally short-lived resources (Ward & Zahavi 1973). This is not to deny that synchrony within colonies could facilitate information transfer about the location of foods that are patchy or ephemeral in availability, and which may be important at different times in the nesting cycle (Ward & Zahavi 1973). However, synchrony may also be important to post-nesting group cohesion and information use about subsequent movements, and nesting opportunities (Jaeger & Jaeger 1980, Galef & Wigmore 1983). The seemingly complex array of migratory routes within the region, the use of traditional nesting areas, and the staggered timing of migration to coincide with local differences in the availability of seeding grasses suggests a learned component in the migratory behaviour of Queleas. Experienced groups may return at the same time each year to areas where they have successfully bred in the past.

Nesting strategy

Ward (1971) pointed out that the advantage of itinerant breeding is to allow Queleas to be multi-brooded, or to rebreed if unsuccessful in the first attempt, in an environment where seeding grasses are patchily distributed, short-lived and susceptible to drought. A nesting strategy that also facilitates the spatial and temporal dispersal of nesting areas, as found in the Ethiopian Rift Valley in 1981 (an area with localized drought from 1978 to 1984), might further serve to assure at least partial breeding success by reducing the impact of locally unfavourable conditions (Wiens 1976). In the Awash Valley, ripening grasses are generally available at lower elevations of the middle Awash before they are available in the upper Awash. This implies that early migrating Queleas must pass through the upper Awash to nesting sites in the middle Awash. If, for instance, Queleas departed the southern Rift *en masse* by the end of July and found insufficient food or standing water in the middle Awash due to low rainfall, the result could be an overall failure of nesting. Assuming that Queleas cannot predict the location or timing of rains, it would seem to be advantageous for the individuals to return to areas where they previously had bred successfully. If they encountered unfavourable nesting conditions, the opportunity would exist to join other groups en route to different areas, or to find alternative nesting sites.

By what behavioural mechanism is dispersal achieved? Given the large area over which they move, it seems unlikely that Queleas sort themselves out into nesting areas based on a regular comprehensive evaluation of resource availability in relation

to bird numbers. Rather, nesting dispersal might be more reliably achieved by segregation among and cohesion within groups, whereby each group returns to the area where it successfully bred in the past. The prompt and synchronous departure of adults from the immediate area of nesting colonies, together with a tendency to segregate by sex and age (Jaeger *et al.* 1979), would contribute to maintaining groups. Learning and collective group information would permit groups to locate scattered nesting habitat more easily (Jaeger & Jaeger 1980). Support for group cohesion in Queleas comes from ringing recoveries in southern Africa, where birds banded together have been recovered together many months later and hundreds of kilometres away (P. Jones pers. comm.). The results of mass-markings undertaken in Kenya and Tanzania during 1984 and 1985 further support group cohesion in Queleas. From one marking site, all 36 recoveries were made in the same area, 100 km away and up to 128 days post-marking. This is not to suggest that regular mixing does not occur in roosts and nesting colonies, but rather that some degree of group cohesion and integrity of information can be maintained from one year to the next.

Parallels exist between the migratory behaviour of the Red-winged Blackbird *Agelaius phoeniceus* in North America and Queleas, suggesting that for blackbirds a similar strategy may operate to ensure widespread, scattered breeding. Red-winged Blackbird migration along the Missouri River is now being studied by mass-marking large spring roosts (Knittle *et al.*, in prep.). The annual breeding migration originates in the south-central United States where Red-winged Blackbirds concentrate in large winter roosts. Millions of Red-winged Blackbirds disperse to nest over a vast area that extends northward through the prairies of west-central Canada. Traditional migratory roosts have been found along this route. Sexual segregation is maintained throughout the migration, with the males arriving first at nesting sites used by them the previous spring. Evidence of long-term group cohesion comes from grouped sightings of birds with similar colour-coded leg streamers from the same tagging site; grouped recoveries of birds ringed at the same time (Dyer *et al.* 1977, Jaeger *et al.* in prep); and a tendency for blackbirds of similar size to roost together during the winter (James *et al.* 1984) which relates to the latitudinal gradient in body size of breeding birds (Power 1970). The above suggests a learned component in the selection of migratory routes and nesting sites of Red-winged Blackbirds, which is reinforced by long-term group cohesion. This is similar to the migratory behaviour that we are proposing here for the Red-billed Quelea.

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Dedication

This work is dedicated to the memory of Peter Ward, whose contributions to the understanding of Quelea ecology formed the basis of this research.

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