Methods for ageing juvenile Red-billed Queleas, *Quelea quelea*, and their potential for the detection of juvenile dispersal patterns

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This paper evaluates potential methods for estimating the hatching dates of free-flying juvenile Red-billed Queleas, *Quelea quelea*, and hence establishing their likely geographical origins and patterns of post-natal dispersal. Based on studies of captive juveniles, the progress of the post-juvenile moult can discriminate up to three differently aged cohorts of young in the same population. Bill colour can help to differentiate very young birds from older ones before post-juvenile moult begins. Skull pneumatization is not useful for precise ageing; it proceeds significantly more slowly in males than females and may not be complete by one year of age. Iris colour remains to be properly evaluated as an ageing criterion. Collections from the Okavango region of northwestern Botswana indicated that juvenile Red-billed Queleas started to arrive there as the local breeding season began. Such birds could only have originated outside Botswana in colonies established in regions of earlier rainfall, probably in those areas of South Africa or Mozambique that form the birds' 'early-rains quarters'. By the beginning of the dry season three months later, the juvenile population of northwestern Botswana comprised up to 40% of such young born elsewhere, indicating widespread long-distance natal dispersal across southern Africa.

INTRODUCTION

Juvenile Red-billed Queleas, *Quelea quelea,* are often responsible for serious crop damage in the vicinity of their natal colonies, where they usually remain for some weeks after their parents have departed to make a further breeding attempt elsewhere. Sometimes, however, the juveniles leave the natal area very soon after fledging and apparently fly long distances in the same direction as their parents. They turn up in areas where the local breeding season has only just begun and may cause crop damage there also (Jones 1989a). In order to gain a better understanding of the patterns of juvenile post-natal dispersal, it is important to be able to identify the likely origins of young birds present in a region during and immediately after the breeding season. A reliable means of ageing young birds is therefore required, so that their date of hatching can be calculated. Information given in a recent handbook of field techniques for quelea workers (Allan 1997) is insufficiently detailed for young queleas to be aged accurately.

Elliott (1981) first proposed a method using the timing and state of progress of the post-juvenile moult to age young Red-billed Queleas in East Africa, which was subsequently adopted by Jaeger *et al.* (1986) in Ethiopia. This paper assesses how reliably the post-juvenile moult can be used in southern Africa. It also evaluates the usefulness of other morphological characteristics (bill and iris colour and the extent of skull pneumatization) that may be used as additional ageing criteria before the post-juvenile moult has started, or when it is difficult to separate juveniles from adults towards the end of the moult.

METHODS FOR AGEING YOUNG BIRDS

Post-juvenile moult

Young Red-billed Queleas undergo a complete post-juvenile moult into the adult eclipse plumage, beginning within 2–3 months of hatching. Moult starts with the feathers of the crown and face and rapidly extends to a full contour moult as the first primary feathers are shed. Primary moult proceeds in the descendent manner typical of passerines. Secondaries and tail feathers do not begin moult until at least 3 or 4 primaries have begun growth, and secondary moult normally finishes shortly after primary moult is complete. The post-juvenile moult is normally followed 1–2 months later by the pre-nuptial contour moult, in which the males acquire the bright breeding colouration on the head and breast. In some juveniles that hatch very late in the breeding season, the two moults overlap. Very rarely (recorded only in eastern African *Q. q. intermedia*), the post-juvenile primary moult may be interrupted to enable the birds to make a precocious breeding attempt before they are one year old (Thompson 1993). Such birds evidently moult directly into breeding dress without passing through an eclipse plumage.

Since primary moult extends over almost the whole period of growth in the other feather tracts, it provides the simplest overall index of moult and is the most easily and consistently recorded on large samples in the field. Only in birds where primary moult is complete is it necessary to check the progress of moult in the secondary feathers. If the innermost one or two secondaries are still growing it indicates that primary moult has only just finished.

Observations on the progress of post-juvenile moult in individual birds were made on small caged samples of three different subspecies, including southern African *Q. q. lathamii* (Table 1). Juveniles were obtained from colonies of *Q. q. quelea* in Nigeria (P. Ward unpubl., GTZ 1982), *Q. q. intermedia* in Tanzania (Elliott 1981) and *Q. q. lathamii* in Botswana (P.J. Jones, unpubl.). All were caged similarly in outdoor aviaries where they were given *ad libitum* supplies of water and millet seed as food. The state of moult was scored for each primary feather of one wing, in which 0 = old feather, 1 = feather missing or in pin, 2 = feather just emerging from sheath, 3 = half-grown, 4 = three-quarters grown, 5 = new feather, giving a total score of 45 for the nine primaries all new (the 10th primary is reduced and was not scored).

West Africa: Q. q. quelea

Data from Lake Chad in northeastern Nigeria collected by P. Ward (unpubl., *in litt.* to Elliott 1981 and GTZ 1982; see also

TABLE 1. Onset and duration of post-juvenile primary moult in three subspecies of Red-billed Quelea. Data obtained from caged samples of *Quelea q. quelea* in Nigeria (Ward in GTZ 1982), *Q. q. intermedia* in Tanzania (Elliott 1981) and *Q. q. lathamii* in Botswana (P.J. Jones, unpubl.)

	n	Timing of breeding attempt	Age at start (weeks)	Age at finish (weeks)	Duration (weeks)
West Africa	?	?	12	26	14½
Q. q. quelea					
East Africa	7	Early	9½–13½	26–32	15–18
Q. q.intermedia	8	Late	9–12	22–27	13–15
Southern Africa	1	Early	?	?	*c.* 20
Q. q. lathamii	5	Late	7–9	19–21	12–13

Meinzingen 1993) indicated that the moult of the body feathers began on the head and back at eight weeks of age (55 days), spreading to the whole body by nine weeks. Contour moult was heavy at 10 weeks. The first primary feather was dropped at 11.5 weeks (80 days) after hatching and primary moult completed at 26 weeks (180 days) after hatching. The total duration of primary moult by this account was therefore 14.5 weeks.

East Africa: Q. q. intermedia

Elliott (1981) provided data from two samples, one of young that hatched on 18 March 1981 near Dodoma, central Tanzania, and another that hatched on 22 May 1981 near Arusha, northern Tanzania (Fig. 1). Birds hatched in March began primary moult at 9.5–13.5 weeks of age (mean 12 weeks), and finished at 26–32 weeks (mean 29.5 weeks). They followed almost parallel moult trajectories with a total period for primary moult of 15–18 weeks.

Young hatched in May began primary moult at 9–12 weeks of age (mean 11 weeks) and completed it when they were 22–27 weeks old (mean 24.5 weeks). The mean duration of primary moult was *c.*13.5 weeks.

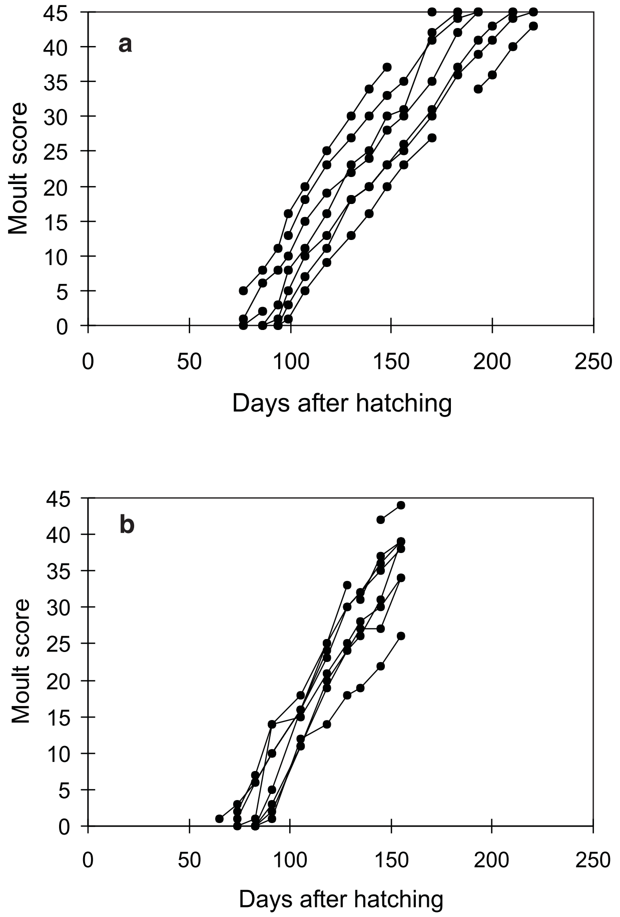

FIG. 1. Progress of post-juvenile primary moult among young Red-billed Queleas that hatched on (a) 18 March in central Tanzania and (b) 22 May in northern Tanzania (Elliott 1981, unpubl.). Lines link successive moult scores of the same individuals.

Southern Africa: Q. q. lathamii

Two small samples are available from northwestern Botswana (Fig. 2). Three independent juveniles were caught on 23 February 1971 in a breeding colony that was at the incubation stage. They began moult in the second half of April and the single bird that survived to complete moult did so at the end of August. Estimation of this bird's mean moult trajectory from Fig. 2 suggests a moult duration of *c.* 20 weeks.

Five newly-fledged, but barely-independent, juveniles were taken on 10 May 1971 from a colony at Makwikwe, on the western edge of the Chobe National Park, where they had hatched on 30 April, i.e. relatively late in the southern African breeding season (Jones 1989b). All five began primary moult between 20 and 30 June at 7–9 weeks of age. They were kept until all but the last one or two primaries had moulted. All followed similar moult trajectories and, by extrapolation, would have completed primary moult at 19–21 weeks of age around 10–25 September. Moult duration would have been 12–13 weeks. A conspicuous feature of late-moulting birds observed in the wild was that they frequently dropped the first four primaries almost simultaneously, whereas earlier birds had only 1–3 primaries growing at the same time (P.J. Jones, unpubl.).

Subspecific differences in post-juvenile moult

It is not possible to tell from these small data sets whether there are any subspecific differences in the timing or rate of post-juvenile moult between *Q. q. quelea, Q. q. intermedia* and *Q. q. lathamii* (Table 1). Ward's data on *Q. q. quelea* were reported secondhand and it was not stated whether his measurements

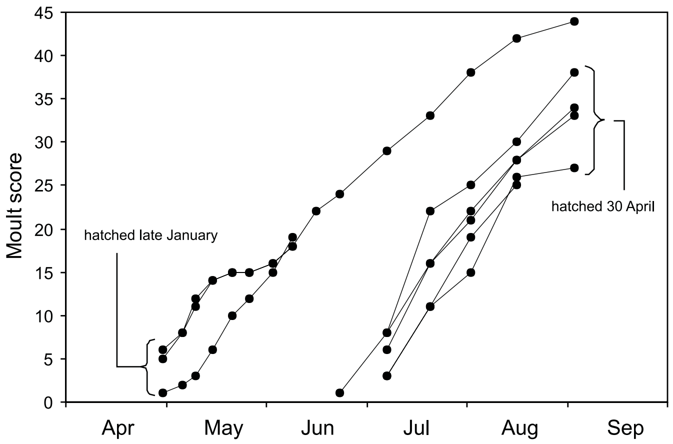

FIG. 2. Progress of post-juvenile moult among young Red-billed Queleas in northwestern Botswana. Lines link successive moult scores of the same individuals. The three earliest birds to moult must have hatched elsewhere in late January. The five later birds hatched in a late colony on 30 April.

TABLE 2. Relationship between bill colour in juvenile Red-billed Queleas and primary moult score during the post-juvenile moult. Data are numbers of birds sampled in June 1971 at Gumare, northwestern Botswana (P.J. Jones, unpubl.).

Moult score	Sex	Bill colour			
		Lavender-horn	Purple-orange	Purple-pink	Pink-red
0	M	9	25	1	1
	F	17	32	4	0
1–5	M		2	3	2
	F		7	14	1
6–10	M		3	11	16
	F		2	15	5
11–15	M			8	5
	F		4	6	5
16–20	M			2	9
	F		1	4	9
21–25	M			2	12
	F			3	6
26–30	M		0	0	1
	F		0	1	3

were made on young born early or late in the season. The single early-hatched *lathamii* moulted more slowly than early-hatched *intermedia* but late-hatched young of these two races moulted at about the same rate.

Accuracy of post-juvenile moult as an ageing technique

Although individuals may vary by as much as two weeks either side of the mean starting date for their cohort (Elliott 1981), it is evident from both the Tanzania and Botswana samples that the start of the post-juvenile moult depends primarily on a bird's age rather than its calendar date of hatching. A small date-effect was apparent in the Tanzania sample, since on average the later-hatched young began moult when about a week younger than the early-hatched sample (11 weeks *versus* 12 weeks old).

A second effect of hatching date was on the rate at which primary moult progressed. The Tanzania and Botswana data sets each contain juveniles hatched early and late in the breeding season. If these small samples are representative, it is clear that late-hatched young completed moult in a much shorter time than those hatched early (Tanzania: 13.5 *versus* 16.5 weeks; Botswana 12–13 *versus* 20 weeks). A similar phenomenon is widespread in temperate species (Jenni & Winkler 1994) and has also been reported in Africa (Jones 1980). The result of this is that later hatched young completed the post-juvenile moult when they were 5–8 weeks younger than early-hatched young. A further consequence is that the end of moult in a quelea population spans a much narrower range of dates compared to its start.

Bill colour

The beaks of juvenile Red-billed Queleas undergo a series of colour changes before they acquire the red colouration of adult birds. The bills of newly independent young birds are horn-coloured with a pale lavender-purple wash. Before the post-juvenile moult begins, the paler parts of the bill acquire an orange colour while the darker parts remain purplish (Table 2). As the moult gets under way the orange becomes pinker. Mid-way through the moult the entire bill becomes pinkish-red and the red deepens as moult nears completion. There is no significant difference between males and females in the timing of these changes (Table 2).

The main usefulness of bill colour is in distinguishing between newly-independent birds that hatched 3–6 weeks previously and those that are 6–10 weeks old and just about to begin moult, but where no signs of moult are yet visible. Once moult has begun this method is much less useful, since bill colour changes relatively slowly and is less readily quantifiable than the moult itself.

Iris colour

In Red-billed Queleas, as in many bird species including other ploceids, the colour of the iris changes with age. Nestlings have the iris grey-black, which changes over the first year of life through grey-brown to the red-brown colour of adult birds. These changes have been claimed to be useful for ageing (GTZ 1982) but we are not aware of any study that has matched iris colour to age. The changes proceed slowly and the different tones merge imperceptibly into one another, so that iris colour cannot be used in any precise way on present knowledge. It would be especially useful if it enabled juvenile birds to be distinguished from adults as they near completion of the post-juvenile moult.

Skull pneumatization

In passerines the extent of pneumatization of the skull is often used in distinguishing juvenile birds from adults. Pneumatization begins after hatching and is usually completed within 2–8 months, depending on the species (Winkler 1979). Thus, if the rate of pneumatization is known, it may be possible to age the juveniles of some species more precisely within their first year of life. In juvenile Red-billed Queleas pneumatization is said to begin at 6–7 weeks of age and to be completed at 6–7 months (Ward 1973; GTZ 1982; Meinzingen 1993), but the accuracy of these timings and their usefulness as an ageing technique have not previously been assessed.

The progress of pneumatization may be scored on live or dead birds according to the proportion of the skull-roof showing the characteristic white, dotted appearance of bilaminate bone contrasting with translucent pink unpneumatized areas. Several scoring systems have been used to record pneumatization. Ward (1973) used a 5-point scale from 0 (completely unpneumatized) to 4 (fully pneumatized). GTZ (1982) and Allan (1997) adopted Ward's illustrations but ascribed an individual score (1–9 and 0–8, respectively) to each of nine successive stages. The results used here are based on data initially recorded on an 11-point scale (0 = unpneumatized; 1–9 = partly pneumatized in 10% increments; 10 = pneumatization complete), that we later grouped for analysis according to Ward's (1973) system.

The skulls of a large number of birds were examined in samples of queleas collected at a roost at Samedupe on the Boteti River,

TABLE 3. Percentages of male and female Red-billed Queleas from Samedupe, northwestern Botswana, at different stages of skull pneumatization at (a) the end of moult (Oct–Nov) and (b) when breeding (Feb–Mar). Juvenile/first year birds were not distinguished from older birds. Pneumatization scores are: 1 = 10–50% complete; 2 = 60–80% complete; 3 = 80–99% complete; 4 = complete.

	Skull score			
	1	2	3	4
(a) Oct–Nov				
Males (n = 246)	10.2	25.6	13.4	50.8
Females (n = 289)	3.5	14.9	10.7	70.9
(b) Feb–Mar				
Males (n = 1206)	8.4	22.0	14.7	55.0
Females (n = 1975)	1.9	11.1	10.3	76.8

Botswana, (20° 07′S, 23° 32′E) between 20 October and 20 November 1971. Unfortunately these could not be separated into first-year and older individuals, because by this date the post-juvenile/post-nuptial moult was all but complete, and all were in fresh adult plumage with some males just beginning the pre-nuptial moult. Iris colour was not known then as a possible ageing criterion (see above) and was not recorded.

Although most birds had fully pneumatized skulls, some had barely begun the process. Males were less advanced than females ($\chi^2_3 = 26.72$, $P < 0.001$; Table 3a). This difference could occur if the proportion of birds less than one year old was greater amongst males than amongst females, but this seems unlikely in such large samples and the same disparity was evident the following breeding season in February and March 1972.

The rate of pneumatization may slow as the process nears completion. In each of five colonies sampled in northwestern Botswana in February–March (Table 3), some breeding males had hardly begun skull pneumatization and significantly more females than males had completed the process ($\chi^2_3 = 195.50$, $P < 0.001$; Table 3). The small increase in the extent of skull pneumatization in each sex since the previous October–November was not significant in either sex (males: $\chi^2_3 = 2.95$, $P = 0.40$; females: $\chi^2_3 = 7.38$, $P = 0.06$, Table 3). These data suggest that if the process had not been completed by the end of the post-juvenile moult, it did not proceed much further, if at all, before the bird's first breeding season. Whether pneumatization might have restarted after this and eventually have become complete is unknown. It follows, therefore, that skull pneumatization alone cannot be used as a reliable indicator of a bird's age.

JUVENILE DISPERSAL IN SOUTHERN AFRICA

Three examples from northwestern Botswana illustrate how these techniques may be used to identify separate age cohorts among juvenile Red-billed Queleas and give some indication of where the birds may have originated:

(i) Three free-flying juveniles were captured at a nesting colony near Makalamabedi (*c.* 20° 10′S, 23° 50′E) in late February 1971 and taken into captivity (see above). They had clearly not hatched in this colony, which was then at the incubation stage, but in a colony that had been established much earlier in the season. These juveniles began primary moult in the second half of April. If, like early-hatched young in Nigeria and Tanzania, they began this moult when *c.* 12 weeks old, they must have hatched in the last week of January in a colony established at the beginning of January. It is almost certain that no colonies had been established anywhere in northwestern Botswana by this early date. These birds must have originated elsewhere, probably several hundreds of kilometres away in South Africa or Mozambique, where breeding normally begins in December–January (Jones 1989b).

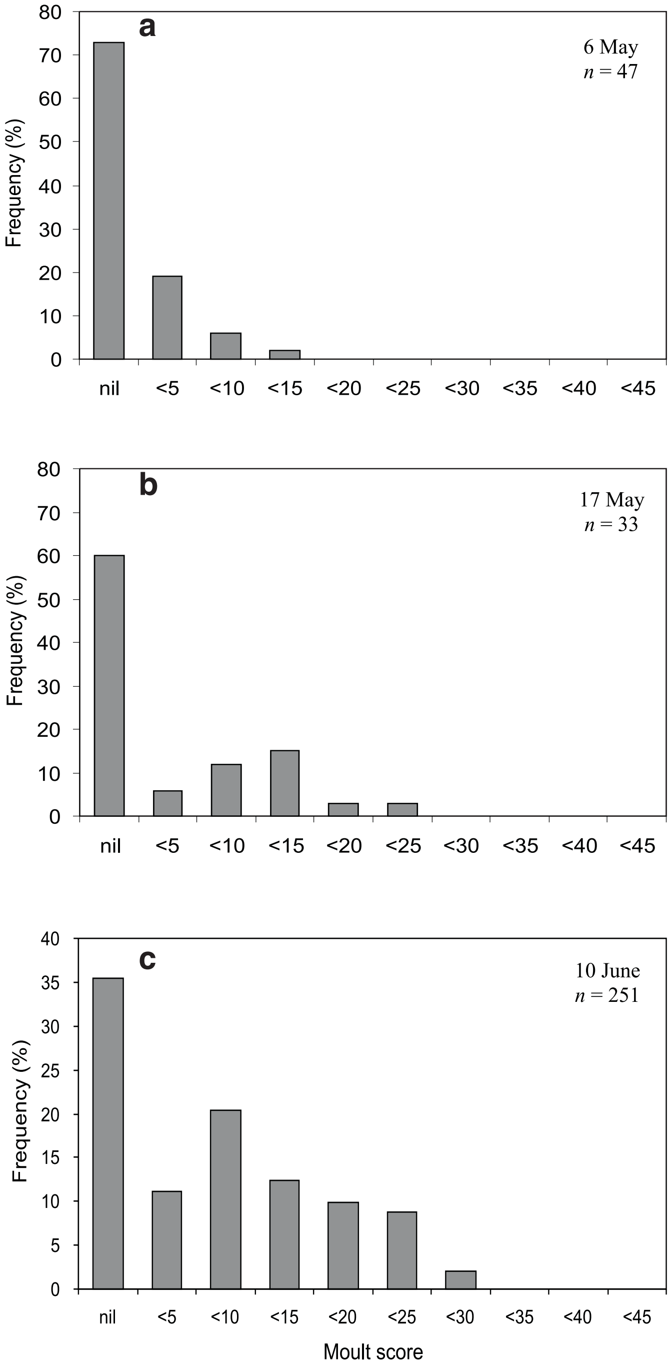

FIG. 3. Frequencies of primary moult scores among juvenile Red-billed Queleas on successive dates in May–June 1971 at Gumare, northwestern Botswana.

(ii) Three samples of juveniles were captured in May and June 1971 at a roost at Gumare (19° 21′S, 22° 10′E) on the western edge of the Okavango Delta. All contained large numbers of birds that had not yet begun post-juvenile moult, as well as others showing a wide range of primary moult scores (Fig. 3). Most birds in the first sample (early May) had not yet begun moult but a small number had primary moult scores up to 15 (Fig. 3a). As in example (i) above, the latter must have hatched in the last week of January in a distant colony. Some of those not yet moulting would probably also have belonged to this early-hatched cohort, but the remainder would have been predominantly locally born young that hatched later.

By mid May, 40% of the birds had started moult and were growing the first 2–5 primaries (Fig. 3b). Their mean moult score

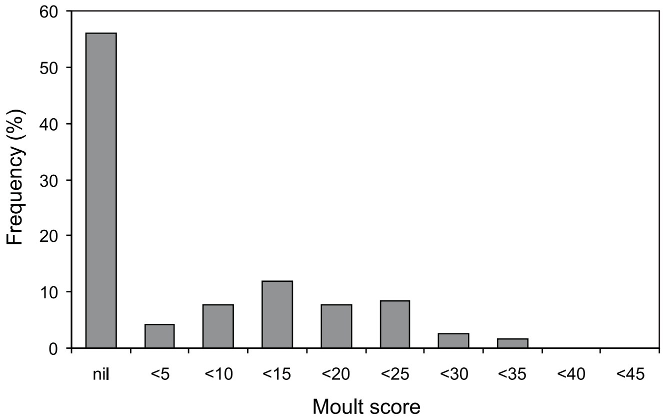

FIG. 4. Frequencies of primary moult scores (n = 118) among juvenile Red-billed Queleas on 6 June 1971 at Kudumane, northwestern Botswana.

(10.5) and the frequency distribution of scores closely matched that expected to have been reached by this date by the birds of distant origin. The remainder, which had still not yet begun moult, were likely to have been less than 12 weeks old and therefore hatched, at the earliest, in late February. Almost certainly they derived from local colonies. Such a clear separation in the frequency distribution between moulting and non-moulting birds suggests that by this date the juvenile population of northwestern Botswana comprised approximately 40% immigrant birds born outside the region and 60% locally born.

The third sample, taken three weeks later in early June, shows the pattern that might be expected from the progress of moult in the interim (Fig. 3c). Most birds were now in moult; those with higher moult scores, as before, were almost certainly immigrants. By this date, however, birds at the earliest stages of moult would have included many of the locally hatched young that had not yet started at the time of the previous sample. This cohort probably comprised most of those with scores of 1–10 and the remainder that had still not started. The latter were almost certainly about to do so, since their bills had begun to turn purple-orange (Table 2). From this sample it is possible to age the younger birds more accurately: all of them would have hatched in late February to early March, undoubtedly from local colonies.

(iii) In support of the inferences made in (ii) above, an identical pattern is shown by data from another juvenile roost sampled in 1971 at Kudumane (19° 09′S, 23° 59′E), on the eastern side of the Okavango Delta 190 km east of Gumare (Fig. 4). On 6 June, 56% of juveniles had still not begun moult, though many were about to do so since their bills had begun to turn purple-orange, and a few with a similar bill colour had just started moult. These would have been locally born young hatched in mid-March and comprised *c.* 60% of the juvenile population. Those already moulting showed a wide range of moult scores, with about 30% with scores between 15 and 25, again suggesting a hatching date in late January and therefore a distant origin.

DISCUSSION

Ageing techniques

The progress of the post-juvenile moult offers the most reliable way of estimating the age of juvenile Red-billed Queleas, though it is subject to several sources of inaccuracy: (i) individual birds born in the same colony may vary by 3–4 weeks in the age at which they begin moult, though it is expected that most will begin close to the mean age. (ii) There may be a one-week difference in the ages at which young from early and late colonies begin moult, though this distinction is not well established. (iii) There is variation in the rate at which young from early and late colonies complete moult, resulting in differences in moult duration of up to eight weeks. The last source of error becomes the most serious later in the moult cycle. Because the spread of dates of moult completion is much narrower than the dates on which moult started, ageing by back-calculation becomes increasingly inaccurate. A further drawback is that it becomes increasingly difficult to separate juvenile birds from adults on plumage characteristics alone as moult nears completion. At best, if most birds in a sample are in the early stages of moult, ageing might be accurate to within 3–4 weeks, giving a useful estimate of the month of hatching and hence a clue to the likely geographical origin of the birds. More cautiously, Elliott (1981) suggested that it should be possible to separate juveniles originating from colonies starting 6–8 weeks apart using moult information alone.

The identification of different age classes of young birds present in a region is made much easier if large samples (>100) are available and if information on other morphological characters is recorded besides the post-juvenile moult. Ideally, samples should be taken on several successive dates (2–4 weeks apart) throughout moult. Successive samples are needed in order to establish when influxes of young from elsewhere may arrive, and large samples ensure that new immigrants can be detected when still at low frequency. For *Q. q. lathamii* in southern Africa, if only a single sample can be collected from a particular locality, it should be taken in June or July. The minimum information obtained from each bird should be the primary moult score and, if it has not yet started, progress of contour moult and bill colour. If moult has already proceeded some way, iris colour should also be recorded as this may help identify juvenile birds. If primary moult is complete, the secondaries should also be checked for the last stages of moult, which would indicate whether primary moult had only just been completed. The extent of skull pneumatization is not useful in this context and does not offer a reliable way of separating first-year and older birds at any time of year, since a significant number of young birds (especially males) do not complete pneumatization before their first breeding attempt.

Juvenile dispersal in southern Africa

Although the post-breeding dispersal patterns of juvenile Red-billed Queleas have not yet been investigated on a large scale anywhere in southern Africa, a preliminary conclusion can be drawn from these analyses. Juveniles from the earliest breeding colonies in southern Africa begin to reach northwestern Botswana in very small numbers by the time adult birds also arrive there and begin their first breeding attempts. By the beginning of the dry season three months later, however, northwestern Botswana has become host to a large influx of young born elsewhere, which may make up as much as 40% of the juvenile population.

The usefulness of such information has been demonstrated in northern Tanzania, where the progress of the post-juvenile moult was first used to age young Red-billed Queleas damaging irrigated dry season wheat, and to identify their likely origin. One of us (C.C.H.E., unpubl.) found that 21% of pest birds came from Kenyan colonies, 34% derived from colonies in central Tanzania, and 46% were birds born locally. In terms of the effectiveness of quelea spraying operations, these data indicated that sufficient juveniles were escaping from the destruction of colonies locally to contribute significantly to the damage. Similar data on the origins of the juvenile birds in dry season aggregations of queleas would also be of value on a wider scale across southern Africa, particularly from areas where cereal crops are susceptible to quelea damage immediately after the breeding season. This information is potentially useful for assessing the extent to which the effectiveness of local quelea control might be undermined by influxes of immigrants from elsewhere.

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