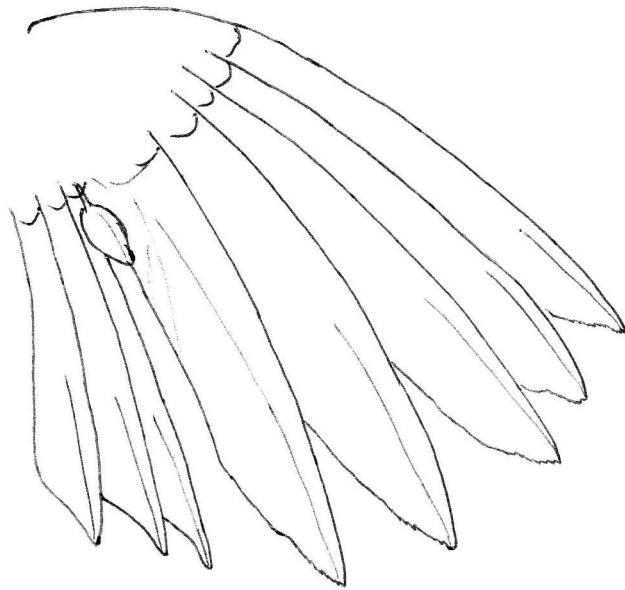# Chapter 4

The Red-billed Quelea in southern Africa: primary moult and the rainfall migration model

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Abstract

The onset and duration of primary moult were investigated for Red-billed Quelea *Quelea quelea* in southern Africa. Duration of moult was shortest in Namibia (75 days), intermediate in Botswana (83 days) and longest in Gauteng Province, South Africa (101 days). The onset of moult was similar in Namibia and Botswana (21 May and 31 May respectively), but considerably earlier in Gauteng Province (23 April). Completion of primary moult was well synchronized, ending in August in all sub-regions. Production of feather mass was uniform and moult speed was adjusted by the number of primaries growing concurrently – fewer feathers grew simultaneously when moult was faster. Red-billed Queleas are thought to migrate relative to the movement of rain fronts, allowing possible multiple breeding events in one season. Two 'rainfall migration models' were evaluated in the light of the results of the primary moult analyses. Queleas are present throughout their range through the year, and a proportion of the population moves short distances in random directions.

Introduction

The Red-billed Quelea *Quelea quelea*, the most abundant bird species in the world, is an extremely mobile species. Endemic to Africa, it is a major pest of small grain crops and is therefore a major threat to subsistence farmers and of economic importance to commercial farmers (Bruggers and Elliott 1989, Mundy and Jarvis 1989). There are three well-defined populations: *Q. q. quelea* occurs in western Africa from Senegal to Chad; *Q. q. aethiopica* in north-eastern Africa from Sudan to Somalia, north-eastern Zaire, Uganda, Kenya and Tanzania, and *Q. q. lathamii* in southern Africa (Craig 2004). Elliott (1989) estimated the post-breeding population to be 1.5 billion birds.

Although millions of queleas are killed each year in control operations, these birds remain abundant and their range continues to expand (Elliott 1989, Mundy and

Herremans 1997). One of the strategies that makes this species so successful is thought to be itinerant breeding, with individual birds nesting successively at different colonies in optimal conditions during a single breeding season (Bruggers and Elliott 1989). This strategy is known as the 'rainfall-migration model', and was developed by Ward (1971), and elaborated by Jones (1989a,b). At each breeding attempt, the species is monogamous and both parents incubate eggs and feed young. Males leave colonies first, and females frequently have well-developed eggs in their oviducts when they leave their fledglings, which are reared to independence three weeks after hatching (Jones 1989c).

Although the Red-billed Quelea is a particularly well-studied species, remarkably little is known about its moult (Oschadleus 2001); Craig *et al.* (2001) investigated primary moult parameters in quelea in the Eastern Cape and Thompson (1988) compared timing of breeding and moult in Kenya. An understanding of the timing and duration of primary moult is important because it provides insights into a key component of the annual cycle of this successful species. Here, the focus is on the moult of the primary wing feathers, because the main annual moult of many other feather tracts takes place within the period of moult of the primaries. The spatial variation of the primary moult parameters (duration and timing of moult) of the Red-billed Quelea *Q. q. lathamii* were considered at a series of localities in southern Africa. These results were placed in the context of the 'rainfall-migration model', which provides the conventional framework for understanding quelea movements.

Methods

Ringing data were submitted by ringers in the electronic format used by SAFRING (South African Bird Ringing Unit). This includes location, date and primary moult (de Beer *et al.* 2001). Sub-regions were chosen with at least 100 records of birds with growing primaries, with records spread through the moult season, especially at the start and end of primary moult. The following sub-regions were used (Figure 1): one degree grid cell 1915 (= 19°S–20°S, 15°E–16°E) which includes all records from Windpoort Farm (near Etosha Pan) in Namibia; grid 1725 which includes all records from Kasane in extreme northern Botswana; all records from Gauteng Province (Gauteng hereafter),

South Africa (four one-degree grids 2527, 2528, 2627 and 2628 with 55 localities). Results from the Eastern Cape (Craig *et al.* 2001) were compared to records from these sub-regions; a similar data set was reanalyzed using the records from grids 3125, 3225, 3324, 3325 and 3326.

The Red-billed Quelea has nine primary feathers (the 10th primary is vestigial), which are moulted from the innermost primary outwards. The relative masses of each primary (as described in Underhill and Summers 1993) were taken from Craig *et al.* (2001). The Underhill-Zucchini moult model (Underhill and Zucchini 1988), developed to estimate the start and duration of primary moult, was applied to the data sets. The data were considered to be of 'type 2' (Underhill and Zucchini 1988), because full moult scores were recorded for each bird and all birds were considered available for sampling throughout the moult period. The parameters of primary moult were estimated using the transformations recommended by Summers *et al.* (1980, 1983), designed to reduce the bias introduced by the fact that the individual feathers are of different masses. The moult index used was percentage feather mass grown (PFMG), calculated from the moult score for the individual feathers according to the method of Underhill and Summers (1993). In addition, this analysis was undertaken to estimate the parameters of moult of each individual primary (Underhill 2003, Underhill *et al.* in press).

Results

2881 ringing records and five recapture records were obtained for adult Red-billed Queleas in the target grid cells in Namibia, Botswana and Gauteng between March 1999 and December 2004; an additional 2970 ringing and 75 recapture records between March 1995 and January 2004 are available for the Eastern Cape, including the records published in Craig *et al.* (2001). Birds were considered to be in arrested moult if both new and old primary feathers were present, and there were no growing feathers. The percentages of birds with arrested moult varied widely: in Botswana, it was 6.1%; in Namibia 0.2%; in Gauteng 1.5%; and 0.4% in the Eastern Cape. These birds were excluded from the primary moult analysis. Of birds in moult, the number of simultaneously growing primary feathers per individual varied by sub-region. In

Namibia, most birds moulted one primary at a time, but about 7% moulted two; in Botswana the proportion moulting two primaries simultaneously increased to 19%; in Gauteng and the Eastern Cape, up to four primaries were moulted simultaneously, with more than half of the birds moulting two primaries (Table 1).

Capture of moulting birds was distributed fairly evenly over the moulting season (Figure 2); this improves the reliability of the moult estimates. In Namibia, duration of moult in adults was estimated to be 75 days (2.5 months) and the mean starting date was 21 May. In Botswana duration of moult in adults was estimated to be 83 days (2.8 months) and the mean starting date was 31 May. In Gauteng duration of moult in adults was estimated to be 101 days (3.4 months) and the mean starting date was 23 April (Table 2).

The Underhill-Zucchini model was applied to individual primary feathers for adult birds (Table 3, Figure 3). There was a high degree of overlap between sub-regions in duration of growth of individual primaries. In Gauteng the individual feathers took between 17 and 36 days to grow, in the Eastern Cape 18 to 29 days, in Botswana 10 to 18 days, and in Namibia 6 to 15 days. In the latter two sub-regions, however, duration of moult could not be calculated for all individual primaries (Table 3).

Using the information in Table 3 for quelea in Gauteng and the Eastern Cape, and simplistically assuming that each feather grows uniformly, the proportion of the total primary mass produced each day was calculated (Figure 4). In Gauteng this varied between 0.57% and 1.46% (apart from one exceptional day when primaries 8 to 10 were all estimated to be growing): the rate was lowest (at 0.57%) when primaries 1 and 2 were growing, and peaked at 1.46% over a nine-day period, when primaries 9 and 10 were growing. In the Eastern Cape, the birds initially displayed a slightly higher relative growth rate, but this then stabilized between 0.51% and 1.04%.

Discussion

Comparison of moult parameters between sub-regions
Primary moult commenced earliest in the Eastern Cape, 2–3 weeks later in Gauteng, and last (6–8 weeks later) in northern Botswana and northern Namibia. This trend is

consistent with the general pattern for southern African passerines, namely that primary moult commences after the completion of breeding, and usually takes place in autumn and winter. The length of the delay across southern Africa is similar to the average delay in the onset of the wet seasons across southern Africa between the south-east and the north-west (Allan *et al.* 1997).

The pattern of duration of moult of individual feathers was unexpected, and varied widely in the different sub-regions (Table 3). In Gauteng the outer primary, which is the heaviest and accounts for 14.8% of total primary feather mass (Craig *et al.* 2001), was the fastest to grow (17 days). The four small inner primaries, accounting for 8.0% to 9.9% of total feather mass, took up to twice as long to grow (25 to 36 days). However, while the inner primaries were being moulted, three or four primaries were often growing simultaneously. While the outer primaries were being moulted, one or two primaries were growing (Table 1, Figure 3).

This moult strategy results in fairly uniform production of feather keratins (Figure 4). A shorter moult duration (i.e. fast moult) was achieved by growing fewer feathers concurrently but growing them rapidly. The outermost primary grows five times faster in Namibia (6 days, Table 3) than in the Eastern Cape (29 days). Zenatello *et al.* (2002) showed that Black Terns *Chlidonias niger* can either moult many primaries at a slow speed, or less primaries at a faster speed. These results are contrary to those found for Common Starlings *Sturnus vulgaris*, which grew more feathers concurrently to achieve shorter moult periods (Dawson 2004). Serra (2002) demonstrated that feather quality was related to moult speed in Grey Plovers *Pluvialis squatarola*.

It was striking that the timing of the completion of moult in the four sub-regions was more synchronized than the commencement of moult. In three of the four sub-regions, the mean completion dates lay between 2 and 8 August, and the mean completion date in northern Botswana was two weeks later (Table 2). This synchronization of completion dates was possible because the duration of Red-billed Quelea primary moult was shortest in Namibia at 75 days, with progressively longer mean durations for birds towards the south-east, with an estimated duration of 124 days in the Eastern Cape (Figure 1, Table 2). In each sub-region, most individual birds would have completed moult by the end of September. Throughout the breeding range of the

Red-billed Quelea in the summer rainfall region of southern Africa, the period September to November is the longest time since the last production of natural grass seeds, and the period when food is least abundant. It is therefore probably the period during which moult should not be undertaken.

The most likely reason for the variation in moult duration is related to the movements of the species. Birds migrating to Botswana and Namibia breed and then start moult, but consequently have less time to complete their moult. A consequence is that birds in Namibia may grow feathers of a lower quality than in the eastern parts of southern Africa; this needs to be investigated further.

Moult in the annual cycle and the rainfall-migration model

Ward (1971) considered that Red-billed Queleas carry out migrations which are related to the progress of rain fronts and consequent availability of food. In southern Africa, Jones (1989a, b) applied this hypothesis to the movements of Red-billed Quelea, and proposed a rainfall-migration model for the species in this region. This model is based on a simplified pattern of the initiation of the wet season across the summer rainfall zone of southern Africa and its impact on the germination of natural grass seed. Along a south-east to north-west transect from KwaZulu-Natal to northern Namibia, the onset of the heavy rains that trigger seed germination is progressively later (Allan *et al.* 1997, Figure 15). Optimal conditions for breeding, namely the availability of fresh grass seed and insects, occur six to eight weeks after the start of the heavy rains. According to this model, quelea undertake a long pre-breeding migration across the rain fronts towards the south-east in November, arrive in areas with good breeding conditions about six-eight weeks after the rains, and start breeding. The breeding cycle takes about seven weeks (nest construction and egg laying overlap and are completed in six days; incubation lasts 9–10 days; the nestling period takes 11–13 days; chicks fledge at age 16 days, commence self-feeding at 19 days, and are independent fledglings within a day or two after this) (Jones 1989c). The emergence of fresh grass seeds progresses steadily towards the north-west. Adults desert breeding colonies as soon as fledglings are independent, move north-west to find places where the heavy rains started six to eight weeks previously, and breed again in good conditions, probably several hundred kilometres north-west of the previous

breeding event. In terms of this model, Red-billed Queleas are described as itinerant breeders, and the north-west movement to successive breeding colonies is known as the breeding migration (Ward 1971, Jones 1989b). The model envisages regular north-west to south-east migrations between South Africa, Botswana and Namibia, over distances in excess of 1000 km (Ward 1971, Jones 1989b).

Because of the enormous variability in the pattern of rainfall events in southern Africa between years, this model is an over-simplification, but the underlying principle of itinerant breeding is likely to be correct (Jarvis 1989). Breeding of the same bird at more than one locality in a single breeding season has not yet been demonstrated in southern Africa, but has been shown to occur in Ethiopia (Jaeger *et al.* 1986).

Jarvis (1989) pointed out that a modified version of the rainfall migration model was more likely to be appropriate; he suggested that the pattern of movement would be on a much shorter scale than that envisaged by Ward (1971) and Jones (1989a, b). The early-summer rainfall pattern in southern Africa entails scattered thunder storms resulting in patchy rain, and Jarvis (1989) envisaged queleas moving between the suitable habitat patches these rains would generate. At the start of the rainy season, the birds would need to locate dry areas where grass seeds had not yet germinated, until such time as they could locate breeding sites. The latter would be places where heavy rain had fallen six to eight weeks earlier, and where green seeds and insects were abundant. Jarvis (1989) suggested that most movements would not be on the classic north-west to south-east axis, but in random directions and over relatively short distances.

The rainfall migration model of Ward (1971) and Jones (1989) was never presented as a partial migration model and it assumed that the overwhelming majority of queleas moved along the north-west to south-east axis. The broad-brush seasonal analysis of the data in the Southern African Bird Atlas Project (Mundy and Herremans 1997) did not support this idea. On a finer scale, Allan *et al.* (1995) used the same data, and split the range of the quelea in southern Africa into 12 areas and found that, at this level, 'quelea are present throughout their range virtually throughout the year'. They found that reporting rates for queleas showed little seasonal variation, apart from the South African lowveld (northern KwaZulu-Natal and the Kruger National Park) where there were higher reporting rates during the summer breeding season, indicating influxes of birds. A

similar pattern of continuous presence was observed in southern Mozambique (Parker 1999), whereas in central Mozambique, unexpectedly, reporting rates were highest in midwinter (Parker 2005). A century ago, Haagner (1905) noted that some quelea were resident in Gauteng while other individuals passed through on migration. These results lend support to Jarvis' (1989) short-distance rainfall migration model. The ringing data on which this paper is based also demonstrated that quelea were present in each of the study areas throughout the year, not just in the breeding season or during the moult period. The small number of recaptures obtained was consistent with the magnitude of the quelea population.

It is impossible to interpret the SAFRING ring recovery data in terms of the long-distance rainfall migration model. Oschadleus (2000a) plotted patterns of recoveries on a monthly basis; most movements were not along the north-west to south-east axis predicted by the rainfall migration model. The overwhelming majority of the 510 recoveries were over distances less than 100 km and were in all directions from the site of ringing. The ring recovery data thus also support the Jarvis (1989) short-distance rain migration model.

Agricultural activities have undoubtedly modified the movement pattern of queleas. Small-grain farming and the development of feed lots for livestock provide food at times when it would otherwise be scarce, so that birds do not need to be as nomadic as in the past (Mundy and Herremans 1997, Whittington-Jones *et al.* 2001). Quelea are obligate drinkers and the development of networks of dams (both small farm dams and large reservoirs) in areas with no open water has enabled queleas to exploit areas in which they could not otherwise have survived. Overgrazing, and consequent bush encroachment in previously treeless areas, have also provided sites for breeding colonies in areas that were previously unsuitable (Jones 1989b).

The geographical pattern of breeding seasonality predicted by the long-distance rainfall migration model is weakly supported by a trend in the timing of breeding; in South Africa it is December to April, in Botswana December to April, and in Namibia January to April (Craig 2004). The later start to breeding in Namibia is more parsimoniously explained in terms of late onset of rains than by the arrival of birds from the south-east on migration.

The two-month delay in the onset of heavy rains in northern Namibia relative to south-eastern South Africa, coincides closely with the difference in the data of the commencement of moult across the region (Table 2). Our results therefore suggest that primary moult takes place immediately after the completion of breeding.

If the long-distance rainfall migration model were correct, movements across southern Africa would generate extensive mixing, and all birds would belong to a single meta-population. One would therefore predict that, apart from the timing of the start of moult which is related to breeding seasonality, moult parameters would be similar throughout the region. This is not the case. The observed regional differences in duration of moult are large, between 75 days and 124 days (Table 2), as are the strategies whereby individual primaries are moulted (Figure 3). The proportion of birds moulting only one primary at a time varied from 93% Namibia to 22% in the Eastern Cape (Table 1). It seems unlikely that regional differences of this magnitude could exist within a single meta-population that is continuously being mixed up by long-distance migration, and more likely to be explained by regional adaptations along environmental clines. Thus the results of this moult study also lend support to the Jarvis (1989) short-distance rain migration model.

Strengths, limitations and extensions of this study

This study benefited from the fact that the moult parameters were estimated at all localities using the same fieldwork protocol; this is a by-product of the series of SAFRING training courses conducted twice-yearly since March 2000 (Oschadleus 2000b). It also benefited from the use of a single statistical model to undertake the statistical analyses of the primary moult data; this has also been highlighted by Serra (2002), who demonstrated the importance of using uniform methods in making fine-scale comparisons of the timing and duration between sites.

The Underhill-Zucchini moult model assumes that the sample of moulting birds is a representative sample of a population of birds. If nomadic behaviour during moult generates a passage of birds through the study site in such a way that populations passing through have different moult parameters, then the data collected at the site would not be

representative of any real population. However, the ring-recovery data provide no evidence that this pattern of movement occurred.

At each study site, data for several years were combined because sample sizes in any single year were small. This is not ideal, because there may be inter-year differences in moult parameters. At best, the consequence of this is that the moult appears less synchronized than it actually is in an individual year. At worst, a large sample of birds from a single year in which moult is particularly early or late can bias the results. This latter scenario is unlikely, because the contributions of data from single days were generally small. The results from each of our study areas are likely to be representative of the average moult parameters at the site.

This analysis has revealed geographical patterns in the timing and duration of primary moult across southern Africa. Data from a selection of sites across the subcontinent would confirm the geographical pattern of timing of moult, and the pattern of duration, which were not anticipated. Further studies of the primary moult of the Red-billed Quelea should concentrate on an understanding of inter-year variation at a study site; this requires sampling at regular intervals throughout the moult period of the population at the selected site over several years.

References

Allan DG, Harrison JA, Herremans M, Navarro RA and Underhill LG 1997. Southern African geography: its relevance to birds. pp lxv-ci. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The atlas of southern African birds. Vol. 1: Non-passerines. BirdLife South Africa, Johannesburg

Allan DG, Harrison JA, Navarro RA and Martinez P 1995. The Redbilled Quelea and non-target birds: insights from bird atlas data. Research Report of the Avian Demography Unit, University of Cape Town, Cape Town

Bruggers RL and Elliott CCH (eds) 1989. *Quelea quelea:* Africa's bird pest. Oxford University Press, Oxford

Craig AJFK 2004. *Quelea quelea.* pp 207-212. In: Fry CH and Keith S (eds) Birds of Africa. Vol. 7. Christopher Helm, London

Craig AJFK, Hulley PE, Whittington-Jones CA and Bonnevie BT 2001. Flying times and flight feathers: patterns of moult in sympatric seedeaters. Ostrich Supplement 15: 66-70

Dawson A 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. Ibis 146: 493-500

de Beer SJ, Lockwood GM, Raijmakers JHFA, Raijmakers JMH, Scott WA, Oschadleus HD and Underhill LG 2001. SAFRING bird ringing manual. Avian Demography Unit Guide 5. Avian Demography Unit, Cape Town

Elliott CCH 1989. The pest status of the quelea. pp 17-34. In: Bruggers RL and Elliott CCH (eds) *Quelea quelea:* Africa's bird pest. Oxford: Oxford University Press

Haagner AK 1905. A further contribution to the ornithology of Modderfontein, Transvaal. Journal of the South African Ornithologists' Union 1(2): 48-56

Jaeger MM, Bruggers RL, Johns BE and Erickson WA 1986. Evidence of itinerant breeding of the Red-billed Quelea *Quelea quelea* in the Ethiopian Rift Valley. Ibis 128: 469-482

Jarvis MJF 1989. Quelea breeding and seasonal distribution in southern Africa. pp 69-83. In: Mundy PJ and Jarvis MJF (eds) 1989. Africa's feathered locust. Baobab Books, Harare

Jones PJ 1989a. General aspects of quelea migration. pp 102-112. In: Bruggers RL and Elliott CCH (eds) *Quelea quelea:* Africa's bird pest. Oxford University Press, Oxford

Jones PJ 1989b. Distribution, populations, and migration patterns of quelea in southern Africa. pp 132-143. In: Bruggers RL and Elliott CCH (eds) *Quelea quelea: Africa's bird pest.* Oxford University Press, Oxford

Jones PJ 1989c. The breeding cycle of *Quelea quelea* and factors initiating breeding. pp 36-49. In: Mundy PJ and Jarvis MJF (eds) Africa's feathered locust. Baobab Books, Harare

Mundy PJ and Herremans M 1997. Redbilled Quelea *Quelea quelea*. pp 573-575. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V and Brown CJ (eds) The atlas of southern African birds. Vol. 2: Passerines. BirdLife South Africa, Johannesburg

Mundy PJ and Jarvis MJF (eds) 1989. Africa's feathered locust. Harare: Baobab Books

Oschadleus HD 2000a. Red-billed Quelea movements in southern Africa shown by ringing recoveries in the SAFRING database. pp 125-135. In: Cheke RA, Rosenberg LJ and Kieser ME (eds) Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Research Institute, Pretoria, South Africa, 24-26 March 1999. Natural Resources Institute, Chatham

Oschadleus HD 2000b. First bird-ringing course held at Witsand Reserve. Bird Numbers 9(1): 14

Oschadleus HD 2001. Bibliography of the African quelea species. Avian Demography Unit, University of Cape Town, Cape Town

Parker V 1999. The atlas of the birds of Sul do Save, Southern Mozambique. Avian Demography Unit, Cape Town, and Endangered Wildlife Trust, Johannesburg

Parker V 2005. The atlas of the birds of central Mozambique. Endangered Wildlife Trust, Johannesburg, and Avian Demography Unit, Cape Town

Serra L 2002. Cold winters vs. long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis squatarola*. Unpublished PhD thesis, University of Cape Town, Cape Town

Summers RW, Swann RL and Nicoll M 1980. Unbending moult data. Wader Study Group Bulletin 30: 12-13

Summers RW, Swann RL and Nicoll M 1983. The effects of methods on estimates of primary moult duration in the Redshank *Tringa totanus*. Bird Study 30: 149-156

Underhill LG 2003. Within ten feathers: primary moult strategies of migratory waders (Charadrii). In: Berthold P, Gwinner E and Sonnenschein E (eds) Avian Migration. pp 187-197. Springer-Verlag, Berlin

Underhill LG, Serra L and Brandao A in press. Progress with the statistical analysis of primary moult. Proceedings of the XXIII International Ornithological Congress, Beijing, China. Acta Zoologica Sinica

Underhill LG and Summers RW 1993. Relative masses of primary feathers in waders. Wader Study Group Bulletin 71: 29-31

Underhill LG and Zucchini W 1988. A model for avian primary moult. Ibis 130: 358-372

Ward P 1971. The migration patterns of *Quelea quelea* in Africa. Ibis 113: 275-297

Whittington-Jones CA, Hulley PE and Craig AJFK 2001. Red-billed Queleas *Quelea quelea* in the Eastern Cape, South Africa: are they settling down? Ostrich Supplement 15: 89-91

Zenatello M, Serra L and Baccetti N 2002. Trade-offs among body mass and primary moult patterns in migrating Black Terns *Chlidonias niger*. Ardea 90: 411-420

Table 1: The number of observations of each primary feather of adult Red-billed Queleas in active moult in different regions of southern Africa, and the percentages of primaries actively moulting while each primary was in moult. The averages are unweighted

(a) Namibia, grid cell 1915

Primary	No. in moult	1 active	2 active
1	1	100.0	0.0
2	3	100.0	0.0
3	9	77.8	22.2
4	9	77.8	22.2
5	13	92.3	7.7
6	23	95.7	4.3
7	32	96.9	3.1
8	34	97.1	2.9
9	18	100.0	0.0
Average		93	7

(b) Botswana, grid cell 1725

Primary	No. in moult	1 active	2 active	3 active
1	2	50.0	50.0	0.0
2	6	33.3	33.3	33.3
3	18	55.6	27.8	16.7
4	29	62.1	27.6	10.3
5	22	77.3	18.2	4.5
6	39	100.0	0.0	0.0
7	37	100.0	0.0	0.0
8	25	96.0	4.0	0.0
9	8	87.5	12.5	0.0
Average		74	19	7

(c) Gauteng Province

Primary	No. in moult	1 active	2 active	3 active	4 active
1	25	8.0	60.0	24.0	8.0
2	44	13.6	47.7	31.8	6.8
3	46	23.9	34.8	34.8	6.5
4	55	30.9	43.6	20.0	5.5
5	44	29.5	59.1	9.1	2.3
6	45	35.6	57.8	6.7	0.0
7	43	25.6	67.4	7.0	0.0
8	35	25.7	68.6	5.7	0.0
9	27	63.0	33.3	3.7	0.0
Average		28	53	16	3

(d) Eastern Cape

Primary	No. in moult	1 active	2 active	3 active	4 active
1	116	14.7	44.0	34.5	6.9
2	141	3.5	51.1	39.7	5.7
3	170	9.4	40.0	45.9	4.7
4	177	9.0	61.0	25.4	4.5
5	220	19.1	67.3	13.6	0.0
6	244	25.4	70.9	3.7	0.0
7	209	27.3	69.9	2.9	0.0
8	205	27.8	69.8	2.4	0.0
9	236	63.1	35.2	1.7	0.0
Average		22	57	19	2

Table 2: Estimates of the primary moult parameters for adult Red-billed Queleas in southern Africa, 1999–2004; * Eastern Cape data from Craig *et al.* (2001)

Region	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completion date	Standard error (days)	n
Namibia	21 May	4.3	37.4	1.9	74.6	4.8	3 Aug	2.7	1163
Botswana	31 May	3.6	35.1	1.8	82.5	4.5	21 Aug	2.6	543
Gauteng	23 Apr	2.6	32.7	1.2	100.9	3.6	2 Aug	2.4	1105
E Cape *	6 Apr	2	36.5	0.8	124	3	8 Aug	1.4	3077

Table 3: Estimates of the primary moult parameters of individual primary feathers for adult Red-billed Queleas in different regions of southern Africa; primary 10 is minute and is omitted

(a) Namibia (n=1163)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
3	2 Jun	3.8	28.1	2.6	7.2	2.3	9 Jun	3.5
4	6 Jun	3.9	30.8	2.9	6.4	2.0	13 Jun	3.6
5	12 Jun	3.9	32.1	3.0	7.8	2.1	20 Jun	3.5
6	18 Jun	3.8	34.9	3.0	12.1	2.5	30 Jun	3.3
7	28 Jun	3.8	39.5	2.9	15.0	2.6	13 Jul	3.3
8	11 Jul	3.5	42.0	2.6	14.2	2.3	25 Jul	3.2
9	24 Jul	3.1	40.1	2.6	6.1	1.5	30 Jul	3.0

(b) Botswana (n=543)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
3	3 Jun	3.1	26.7	2.1	12.0	2.6	15 Jun	3.0
4	10 Jun	3.3	30.9	2.1	18.3	3.0	28 Jun	3.0
5	23 Jun	3.3	34.6	2.5	12.0	2.4	5 Jul	3.1
6	6 Jul	3.3	35.4	2.5	17.5	2.6	24 Jul	2.9
7	22 Jul	3.2	38.8	2.9	14.8	2.4	6 Aug	2.9
8	5 Aug	3.0	39.3	3.2	9.6	1.9	15 Aug	2.9

(c) Gauteng Province (n=1105)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	19 Apr	3.5	42.3	2.5	24.9	3.3	14 May	3.2
2	19 Apr	3.4	39.4	2.3	35.0	3.5	24 May	3.0
3	29 Apr	3.3	37.5	2.1	34.6	3.4	2 Jun	2.9
4	10 May	3.1	36.4	1.9	36.2	3.3	15 Jun	2.8
5	26 May	3.2	38.8	2.0	29.6	3.1	25 Jun	2.9
6	8 Jun	3.1	37.0	1.9	28.6	3.0	7 Jul	2.8
7	22 Jun	3.0	34.7	1.8	26.7	2.9	18 Jul	2.6
8	5 Jul	2.9	31.9	1.7	22.9	2.7	27 Jul	2.5
9	18 Jul	2.9	32.8	1.8	17.2	2.4	4 Aug	2.5

(d) Eastern Cape (n=2738)

Primary	Mean starting date	Standard error (days)	Standard deviation (days)	Standard error (days)	Duration (days)	Standard error (days)	Mean completing date	Standard error (days)
1	9 Apr	2.3	30.7	1.4	17.8	1.9	27 Apr	3.2
2	12 Apr	2.3	31.3	1.4	20.0	1.9	2 May	3.0
3	17 Apr	2.2	32.7	1.5	24.6	2.0	12 May	2.9
4	27 Apr	2.1	34.1	1.6	25.1	1.9	22 May	2.8
5	10 May	2.0	35.6	1.6	26.8	1.9	5 Jun	2.9
6	26 May	1.7	34.0	1.6	22.9	1.7	18 Jun	2.8
7	11 Jun	1.8	40.4	1.5	23.4	1.7	4 Jul	2.6
8	27 Jun	1.8	40.1	1.4	25.4	1.7	22 Jul	2.5
9	10 Jul	1.7	39.3	1.3	29.2	1.7	8 Aug	2.5

Figure 1: Capture sites of adult Red-billed Queleas in selected one degree grid cells, 1995–2004. Black dots in the grid cells show sites from which primary moult data were obtained; the three Eastern Cape grids show the ringing sites that Craig *et al.* (2001) used. All the quarter-degree grid cells in southern Africa in which Red-billed Queleas were recorded during the Southern African Bird Atlas Project are shaded (Mundy and Herremans 1997)
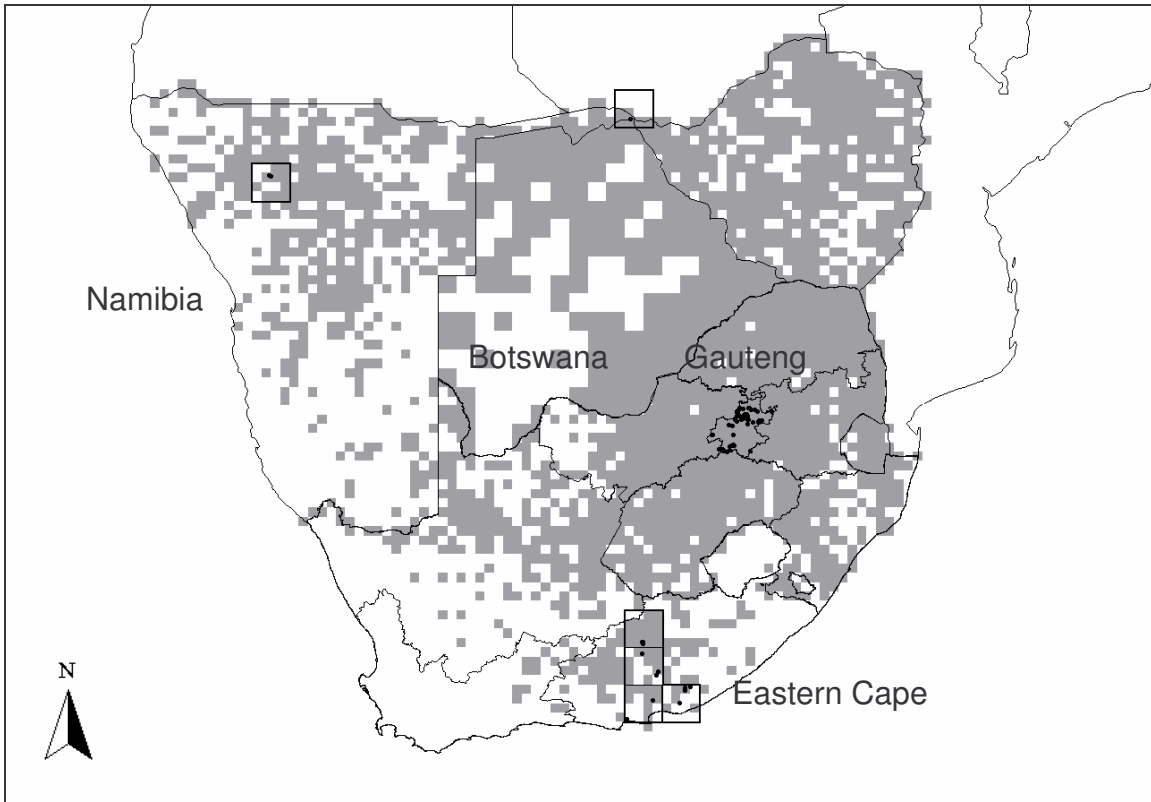
Figure 2: Timing of primary moult for adult Red-billed Queleas in three regions in southern Africa; the solid diamonds represent relative feather mass values by date; the solid diagonal line joins the estimated mean start and end dates of moult, while the diagonal dotted lines show the approximate 95% confidence intervals of moult scores on any given date

(a) Grid cell 1915, Namibia
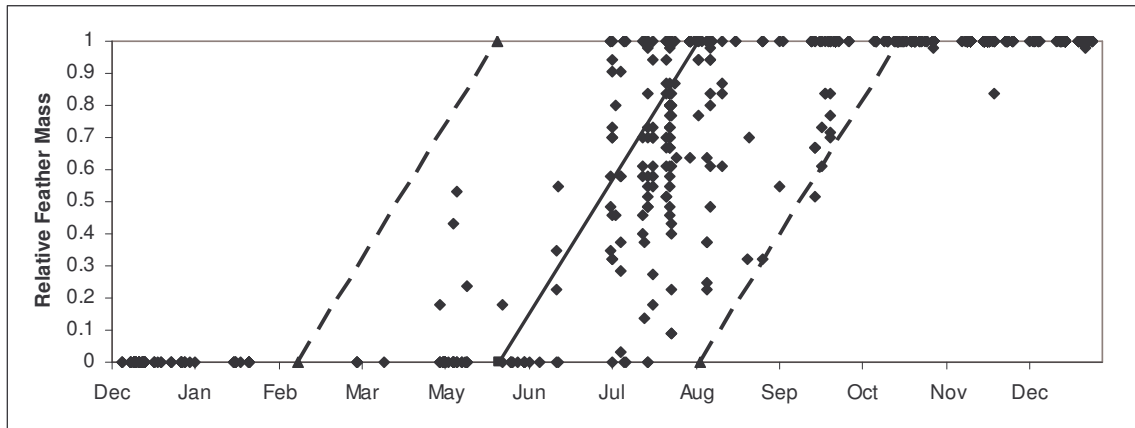
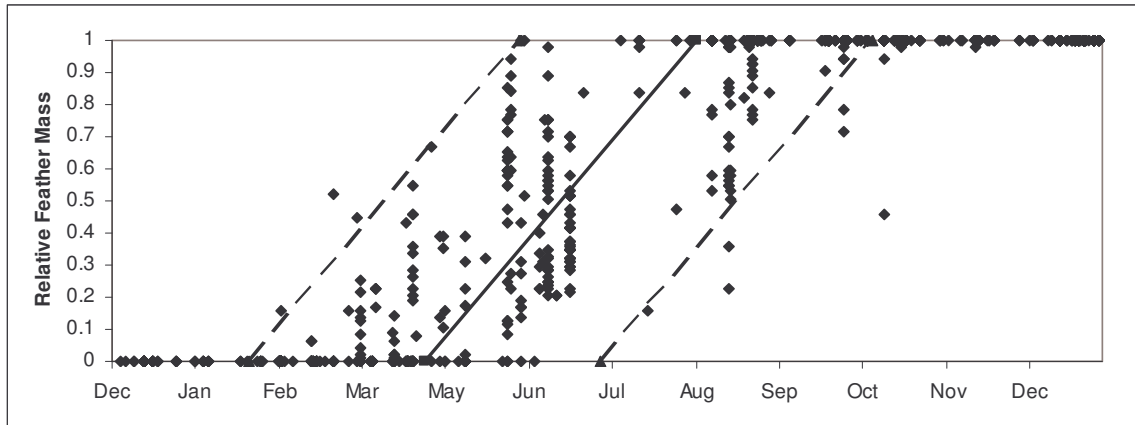(b) Grid cell 1725, Botswana
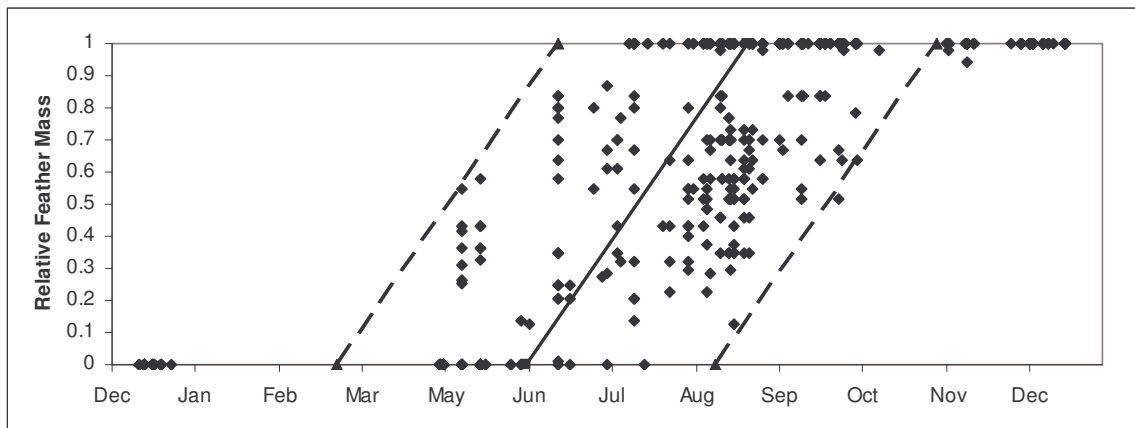
(c) Gauteng Province, South Africa

Figure 3: Individual primary growth of adult Red-billed Queleas in different regions in southern Africa; crosses indicate the dates of the start and end of moult for each primary feather, and distances between pairs of vertical lines indicate standard errors for nine primaries; data in Table 3
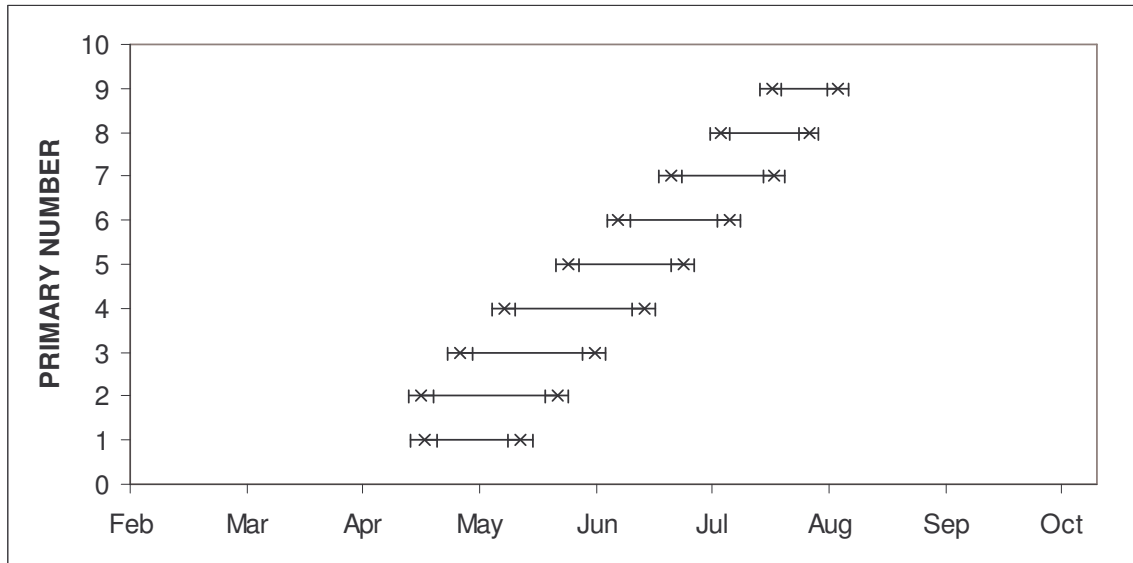
(a) Individual primary growth of adult Red-billed Queleas in Namibia
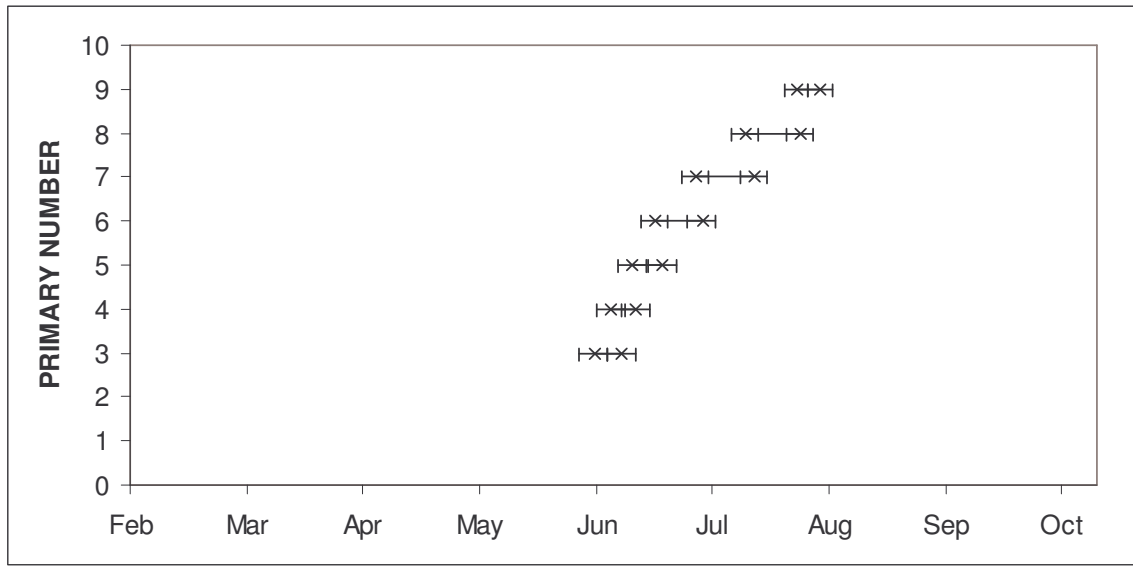
(b) Individual primary growth of adult Red-billed Queleas in Botswana
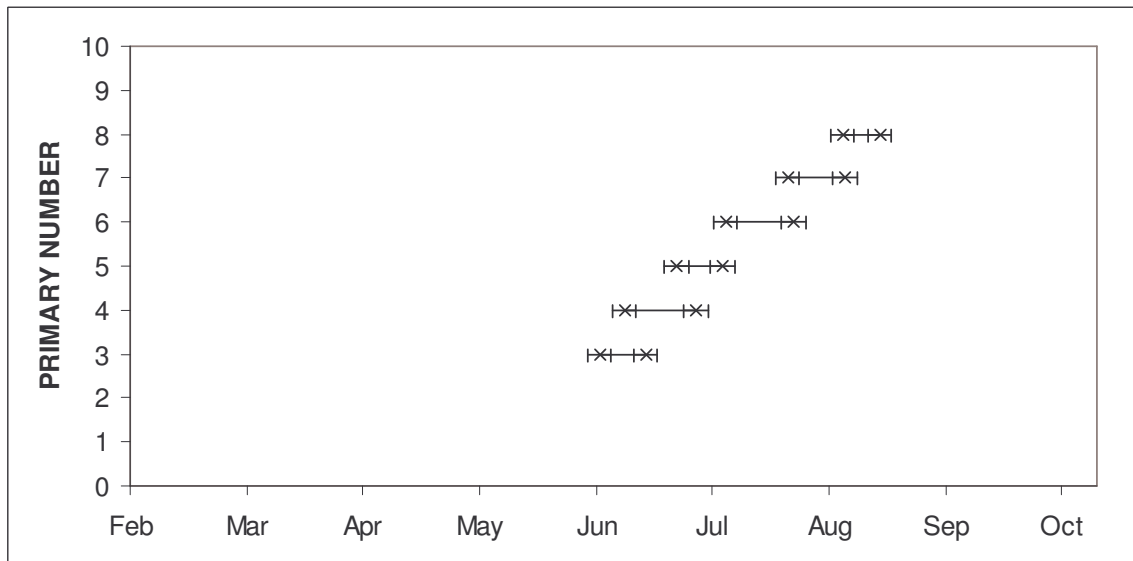
(c) Individual primary growth of adult Red-billed Queleas in Gauteng Province

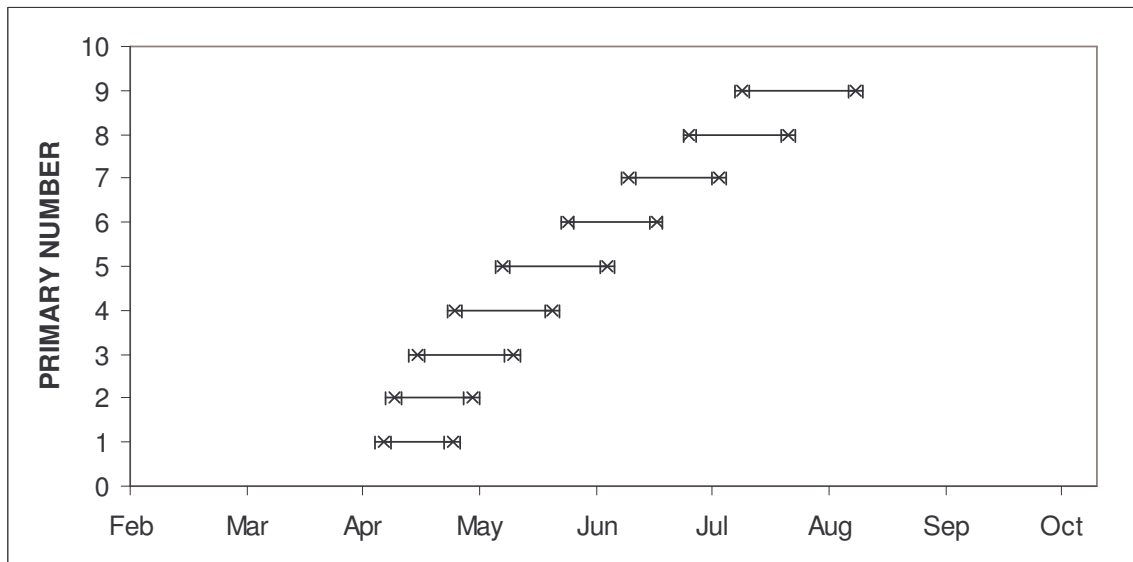(d) Individual primary growth of adult Red-billed Queleas in the Eastern Cape

Figure 4: Model of the relative amount of the total primary mass produced each day for adult Red-billed Queleas in two regions in South Africa, the Gauteng Province (crosses) and the Eastern Cape (closed diamonds)