

Forecasting suitable breeding conditions for the red-billed quelea *Quelea quelea* in southern Africa

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Summary

1. Red-billed queleas *Quelea quelea* are major pests of small-grain crops throughout sub-Saharan Africa. When conditions permit, birds breed in vast colonies which are targets for control operations. Queleas are intra-African long-distance migrants whose complex movements vary annually according to variations in rainfall patterns. An ability to forecast where and when colonies could be established will greatly improve the efficiency of control measures. We describe such a forecasting model for the southern African subspecies *Q. q. lathamii*.

2. The model is based on and provides a partial test of the conjectured rainfall–migration model of Ward (1971), whereby quelea movements are determined by rainfall patterns and grass seed availability. We consider that a threshold quantity of rainfall (shown here to be *c.* 60 mm) within any 2 weeks at the start of the wet season is necessary to cause annual grass seeds to germinate, forcing queleas to emigrate. Only if rainfall exceeds another threshold (240 mm within a 6-week span and at least 6 weeks elapsed after the 60-mm threshold had been exceeded), allowing production of fresh seed, can queleas return and commence breeding. Birds may breed again in the same season by undertaking further long-distance ‘breeding migrations’ to areas where sufficient rain had fallen even later.

3. Using only estimates of rainfall derived from satellite data, we describe a simple spatio-temporal model for southern Africa to show at weekly intervals those areas where (a) the wet season has not yet started; (b) the early rains migration threshold has been exceeded; (c) the threshold to permit breeding has been exceeded; and (d) conditions are no longer suitable for new colonies to be established.

4. *Synthesis and applications.* The model was run for three seasons and performed well compared to an expected null distribution of breeding colonies among quarter-degree grid squares. In 2002/2003 and 2004/2005, but not in 2003/2004, quelea colonies were reported significantly more often in grid squares where the model had predicted breeding to be possible. However, in a more refined analysis of a smaller subset of colonies for which precise dates of their establishment were known, their spatio-temporal distribution matched predictions in 95%, 85% and 99% of grid squares, respectively, over the three breeding seasons. These success rates show that predictions from the model, the first of its kind for any African bird, can aid the planning of quelea control strategies.

Key-words: bird pest control, forecast, migration, model, quelea, rainfall, satellite

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Introduction

The red-billed quelea *Quelea quelea* Linnaeus is a granivorous weaver-bird that occurs at very high populations, up to 1500 million birds in sub-Saharan Africa (Elliott 1989a). They are long-distance migrants, moving up to 3000 km (Oschadleus 2000) in response

to regional rainfall regimes and the availability of their preferred food, the seeds of annual grasses and, during the breeding season, larval insects. When grass seeds are unavailable but small-grain cereal crops are present, queleas will attack crops and have hence gained notoriety as one of Africa's worst pests, causing up to US\$70 million worth of damage per annum at 2005 prices (Elliott 1989a,b). Some countries control queleas by the destruction of roosting areas using explosives or by the spraying of organophosphate pesticides, from aircraft or the ground, onto breeding colonies and night roosts. In an average year in South Africa alone, for example, there are 173 separate control operations, each one covering *c.* 7 ha, with a total kill of *c.* 50 million birds (Willemse 2000).

Most control operations are focused on roosts of non-breeding birds that threaten commercial grain crops, especially wheat and rice grown under irrigation. In such areas, rapid communication systems between farmers and control teams, and efficient reporting methods are already in place. Damage to subsistence crops such as millet and sorghum, however, is caused by juvenile birds that have fledged recently from breeding colonies established in relatively inaccessible areas remote from the croplands themselves and which consequently remain unreported. No data are available on an annual basis from savanna grasslands on the timing of development of the grass seeds and larval insects required by breeding queleas, and there is no prospect of any ground-based monitoring system being developed at the necessary geographical scale. Pest control units therefore have no information on quelea abundance until they receive a complaint of damage from farmers, so control operations are driven necessarily by damage reports. This may mean that control operations are not well timed and a whole crop can be lost while farmers wait for a control team to arrive. If quelea colonies could be detected earlier by the provision of timely information about the suitability of local breeding conditions, they could be controlled more efficiently to reduce crop losses.

Regional differences in the timing and distribution of rainfall mean that the migration systems of red-billed queleas are complex and are complicated further by annual variations in rainfall patterns (Jones 1989a). Quelea movements are therefore often seen as unpredictably nomadic and impossible to forecast. However, the migrations can be understood in general terms within a 'rainfall-migration model' that was first proposed by Ward (1971). Here we test this rainfall-migration hypothesis and show that it is possible to model the birds' breeding activities using information on rainfall alone. We have devised a computer model using spatio-temporal information on rainfall obtained from satellite imagery to predict where and when populations of the southern African subspecies of red-billed quelea *Q. q. lathamii* might breed and which regions they may be expected to avoid. It is intended that such forecasts will help government control teams

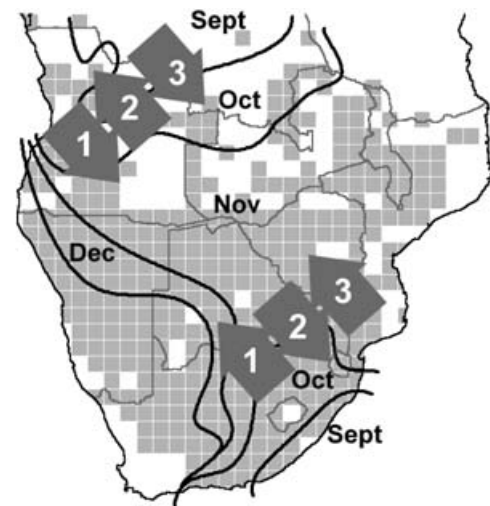


Fig. 1. Schematic map of the timing and directions of red-billed quelea movements in relation to rainfall (Dallimer *et al.* 2003). Contour lines indicate the start of the wet season (modified from Thompson 1965). Arrows indicate: (1) birds forced out of early rains areas when grass seed germinates in September–October; (2) birds forced out of late-rains areas by seed germination in November–December and perform long-distance migration back over rain front; (3) birds perform breeding migration *c.* 6 weeks behind rain front seeking conditions suitable for breeding. Grey shading indicates 1° grid squares where queleas have been recorded, although not necessarily breeding (Magor & Ward 1972; Venn *et al.* 1999).

within the Southern African Development Community (SADC) to target pre-emptive control operations against nesting colonies more effectively. Although there are other migration models based on atlas data (Harrison *et al.* 1997; Griffioen & Clarke 2002) and models linking weather and bird migration (e.g. Shamoun-Baranes *et al.* 2006), this is the first attempt to model explicitly the timing of migration and breeding of any African bird.

The model

RATIONALE

The basis of the model is the conjectured migration pattern of queleas in southern Africa first proposed by Ward (1971) and elaborated by Jones (1989b). Within this pattern, the timing and distribution of rainfall and the resultant growth of annual grasses is the main determinant of the birds' movements. As shown schematically in Fig. 1, when the rains begin and grass seed germinates, queleas are forced to become nomadic, moving ahead of the rain front to any remaining dry areas where ungerminated seed is still available. By late November grass seed has germinated everywhere across the birds' range in the interior of southern Africa, leaving queleas no option but to perform a long-distance migration back across the rain front to the first areas to have received rain (termed the 'early rains migration' by Ward 1971). Here, by now, fresh

seed and the insect prey required for breeding (mainly caterpillars and grasshopper nymphs) are available in large quantities, providing conditions suitable for the first breeding attempt of the season. The southern African subspecies of red-billed quelea appears to comprise a single interbreeding population (Dallimer *et al.* 2003). The question of a 'migratory divide', which splits the southern African quelea population into two subpopulations, one heading for areas of early rain in north-west Angola and the other aiming for similar areas in Mozambique and South Africa, is not fully resolved (Dallimer & Jones 2002), but it does not affect the model.

On arrival in the early rainfall areas, some birds breed immediately while others come into condition more slowly and begin breeding later. As soon as the young from these first broods fledge, the adults continue with what now becomes their 'breeding migration', returning in the reverse direction towards areas of later rain in the southern African interior, where fresh grass seed (and insects) are now becoming available. Along the route of this breeding migration birds can breed wherever suitable conditions of grass growth have occurred, avoiding any areas of drought. Some places provide good breeding conditions reliably for queleas in most years, even under a variable rainfall regime, and can be regarded as traditional breeding sites to which birds return year after year. Other areas may be occupied only if the traditional sites prove unsuitable, or only in years of above-average rainfall. Areas that are suitable for breeding in all respects may remain unoccupied in a particular year if the birds first settle elsewhere.

THRESHOLDS FOR RAINFALL AMOUNT AND TIMING

The start of the rains and early rains movements

The threshold amount of rainfall needed to cause sufficient widespread germination of grass seeds and force queleas to move elsewhere is about 60 mm. This is based on the cumulative amount of rain, between 53 and 69 mm, known to have fallen immediately before mass emigrations of birds that have been directly observed in east and southern Africa (Table 1). Because the very first rainfall is sometimes followed by a more or less

prolonged dry spell that negates its effect, we have assumed that the threshold 60 mm must fall within a 2-week period to cause grass seed germination.

Breeding

Information on the thresholds of rainfall required to permit breeding by quelea is more complicated, as this requires sufficient rainfall to have fallen and sufficient time to have elapsed since the first germination of grass seeds. Luder (1985) devised a set of criteria for deciding when a season had started (a minimum of 35 mm falling in 3 days and no continuous dry spell of 2 weeks within a month of onset) and recommended that evidence of quelea breeding should be sought 5 weeks after the criteria had been met. Data in Gaston (1973) and Gaston & Lamarque (1976) suggested that c. 300 mm of rain is sufficient for the development and seeding of annual grasses (and the emergence of larval insects) needed to permit colony formation but that, depending on different water absorbance rates associated with different soil types, as little as 200 mm or as much as 450 mm might be necessary.

Data obtained during this study suggest that breeding can take place only if more than 240 mm of rain have fallen and at least 6 weeks have passed since the initial 60 mm threshold for the start of the early rains migration has been exceeded, i.e. 300 mm in total. For instance, the 60 mm threshold had been exceeded by the end of November 1971 at Maun in Botswana, where a further 354 mm fell during December 1971 and January 1972, after which many colonies were located from 10 February onwards (Jones & Ward 1976). Further evidence for this threshold was derived from observations in northern Namibia at two sites less than 50 km apart (Alwyn Farm, 19°18'S; 18°51'E and Wilde Farm, 19°10'S; 18°45'E) over four seasons from 1995–96 to 1998–99 (M. Dallimer, personal communication). In 1995–96 and 1997–98, the cumulative rainfall was below 240 mm and no queleas bred at either site. The threshold was exceeded in 1996–97 at both sites (525–553 mm) and grass growth was good but no queleas bred that year either, presumably because the birds stopped elsewhere along the route of their breeding migration where rainfall had also been good. In 1998–99, however, red-billed queleas bred at both sites. At Alwyn Farm, 390 mm had fallen by 28 March and a

Table 1. Cumulative amounts of rainfall (mm) known to have fallen immediately preceding mass emigrations of red-billed queleas observed in east and southern Africa. Rainfall data obtained from the Zimbabwean Meteorological Services and the World Climate Global Climatic Change Data CD-ROM (Chadwyk-Healey Ltd, Cambridge)

Taxon	Country	Site	Date	Source	Rainfall (mm)
<i>Q. q. lathamii</i>	Botswana	Samedupi	November 1971	Ward & Jones (1977)	66.5
<i>Q. q. intermedia</i>	Tanzania	Arusha	November 1969	Ward & Jones (1977)	69.0
<i>Q. q. intermedia</i>	Tanzania	Makuyuni	November/December 1970	Ward & Jones (1977)	68.0
<i>Q. q. lathamii</i>	Zambia	Zambezi escarpment	Mid-November 1960	Tree (1962)	> 53.1
<i>Q. q. lathamii</i>	Zimbabwe	Bulawayo	23 November 1997	This study	67.0
<i>Q. q. lathamii</i>	Zimbabwe	Norton	18–19 November 1998	Dallimer (2001)	61.9

colony was founded *c.* 1 April. At the other site, Wilde Farm, the cumulative total by 25 March was 371 mm, and queleas had established a colony by the end of March.

End of the breeding season

As described above, sites that become suitable for breeding may remain unoccupied because birds have already discovered equally suitable places elsewhere to breed. Only after earlier breeding attempts are completed can birds occupy areas of later rainfall but, even then, they will do so only if the area has only recently become suitable. If the grass seed has already matured and fallen from the seed heads, it becomes much less readily available to queleas and, by this time, caterpillars and grasshopper nymphs have become adults and are unavailable as prey. Suitable breeding conditions are therefore ephemeral and the window of opportunity in any one place is short; for the purposes of the model, we considered this to be 6 weeks. Queleas seeking new nesting areas will bypass such places and move on further along the line of the breeding migration to areas where the rains had begun even later. Such a leap-frogging process will continue until no more areas are suitable to receive birds that might be ready to make a further breeding attempt, and the breeding season ends.

MODEL STRUCTURE

The model was based on that used successfully for forecasting outbreaks of African armyworm *Spodoptera exempta* in Tanzania (Tucker & Holt 1999; Holt *et al.* 2000). The rule-based forecasting model, incorporating state changes by logical 'if-then' rules, was described conceptually, before any programming was started, by Jones *et al.* (2000).

The subspecies *lathamii* of the red-billed quelea is confined to southern Africa, so we included only the continental area between 5°S and 35°S latitude and 11°E and 41°E longitude in the model. The spatial scale chosen initially was 1° × 1° squares but after a trial season in 2001/2002 the resolution of the model was improved for 2002/2003 to quarter-degree squares (0.5° × 0.5°). Time steps were 1 week throughout. Due to the absence of sufficient reports from synoptic weather stations, we utilized rainfall estimates derived from Meteosat Cold Cloud Duration (CCD) data. The model accumulated rainfall data throughout a quelea season (September–May), starting at the beginning of September (calendar week 36, model week 1).

The values of variables used in the final version of the model were chosen in the light of calibration exercises that involved changing the values of different parameters to achieve the best fit with the observed events in the trial season 2001/2002 and again in 2002/2003. For details of the values that were varied and the combinations used see Appendix S1 in Supplementary material. The rainfall estimates were derived solely from satellite

thermal infrared data, which provided estimates of cloud top temperature (CTT). Rainfall was estimated from this on the assumption that high (cold) clouds are more likely to produce rainfall. The Cold Cloud Duration (CCD) value for each satellite image pixel was derived as the number of hours during a day when the CTT was lower than a fixed threshold, in this case –38 °C. The CCD was then converted to a rainfall total using the Geo-stationary Operational Environmental Satellite (GOES) Precipitation Index of Arkin & Meisner (1987) for which 1 h of CCD equates to 3 mm of rain. The value from which it was judged whether the threshold had been exceeded was the average of the values for each pixel within the grid square, but in earlier trials the maximum value was used. Other parameters that were varied were the quantity of rain needed for the second (breeding) threshold, the period during which rain could accumulate and the period between this threshold having been exceeded and the area becoming unsuitable for breeding.

The model was programmed in a Microsoft EXCEL spreadsheet in which worksheet cells represented every 1-degree square for the trial season 2001/2002 and every quarter-degree square for subsequent years. The cell value was given by a formula that implemented the above model criteria; for fuller details see Venn, Cheke & Jones (2003). The model was run each week of each season and seven days of CCD values were input for every run.

CCD files were acquired from the Meteosat satellite using the Bradford University Remote Sensing Ltd Primary Data User System and converted to Image Data and Analysis format. The files were displayed in WinDisp image processing software, which was used to determine either the maximum or mean pixel value within each grid square, and the data were then read into EXCEL to form the basic CCD data file for each week. The CCD values were plotted for each day of the week and summed for the current week's values. The previous 7 weeks' values were also required and were stored in separate worksheets. The previous week's model was then opened in EXCEL and a macro was run that deleted the CCD data from the model and copied each week's CCD and model data into the previous week's worksheet. The current week's CCD data were then copied into the 'empty' model and these were saved as the new model for the current week. For each square, the following questions were asked at the end of each week:

1. What was the total rainfall during the current week?
2. What was the total rainfall during the current week plus the previous week?
3. What was the total rainfall during the current week plus the previous 5 weeks?

Using the above data, the model then invoked the following algorithms:

Algorithm 1: if the total rainfall during the current week in a particular square *or* if the total rainfall during

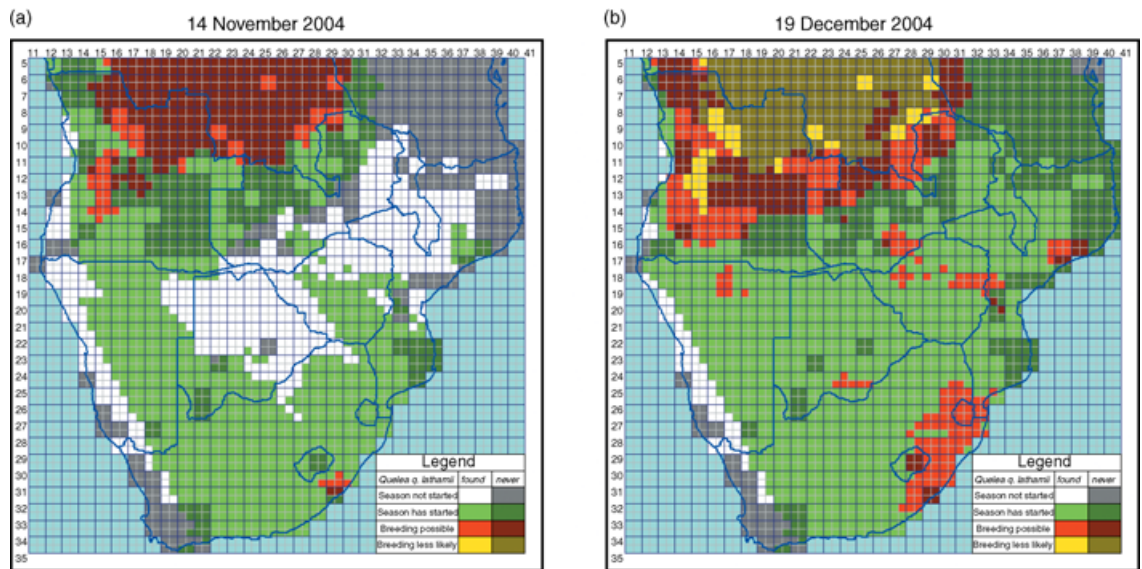


Fig. 2. Output of model for (a) week ending 14 November 2004 and (b) week ending 19 December 2004. White areas: season not yet started; green areas: season started as 60 mm rainfall threshold exceeded; red areas: where conditions are suitable for breeding as 240 mm has fallen within 6 weeks of the 60 mm threshold being exceeded; yellow: sites less suitable as 6 weeks have passed since area became suitable (red).

the current week plus the previous week in a particular square > 60 mm, then the season starts in that square. This is because the threshold of 60 mm has been exceeded and queleas would have been forced to emigrate from that square. To signal the start of the season in a square, it was changed from white to green on the output map (Fig. 2a,b).

Algorithm 2: if at least 6 weeks have elapsed since the season started in a square and the total rainfall during the current week plus the previous 5 weeks in that square > 240 mm (additional to the 60 mm already fallen, giving an overall total of 300 mm necessary for breeding) then breeding is possible in that square. On the output map, a square was changed from green to red (Fig. 2a,b).

Algorithm 3: if 6 weeks have elapsed since breeding was first possible in a square, it is now less suitable for the initiation of breeding (but breeding birds may persist there). On the output map, a square was changed from red to yellow (Fig. 2b).

To visualize the model results, output maps (see Fig. 2a and b for examples) were created as bitmap images from the EXCEL output and these were pasted into Natural Resources Institute websites (<http://www-web.gre.ac.uk/directory/nri/quel/> and <http://www.nri.org/quelea/>) where data have been archived. Since 2003, the model has also been run by the Regional Remote Sensing Unit of the Southern Africa Development Community (SADC), whose output using a -40 °C threshold for CTT has been displayed on another website (http://gisdata.usgs.net/sa_floods/files/region/quel/).

MODEL VALIDATION

Validation of the model was based on the dates and coordinates of breeding colonies reported to agricultural departments and control teams by farmers. Reporting was not systematic and coverage was certainly incomplete. Thus, areas remote from agriculture and all of some countries (e.g. Angola) and parts of others (e.g. Mozambique, Zambia) were not covered. As far as we could tell, reporting of colonies was unbiased in that those areas where sufficient rain had fallen to trigger breeding were not deliberately searched for colonies.

In order to estimate the overall success of the model in correctly predicting that breeding should occur only in those squares in which sufficient rain had fallen, we tested the relative frequency with which colonies had been reported amongst suitable (> 300 mm rainfall within the model's time constraints) and unsuitable (≤ 300 mm) grid squares against a null model in which their expected distribution was derived from the relative frequencies of all squares where sufficient or insufficient rain had fallen. Although red-billed queleas have been recorded over much of the southern African subcontinent outside the breeding season (Fig. 1), many areas do not hold suitable breeding habitat and others remain unknown. We therefore restricted this analysis to the 368 quarter-degree ($0.5^\circ \times 0.5^\circ$) squares where *Q. q. lathamii* are known to have bred in the past (Fig. 3).

We also examined the timing of colony establishment in relation to when the 300 mm rainfall threshold had been reached. For some colonies there was uncertainty about the exact timing of breeding as no information on the state of the colony was provided when it was reported. If information such as nest-building activity, presence

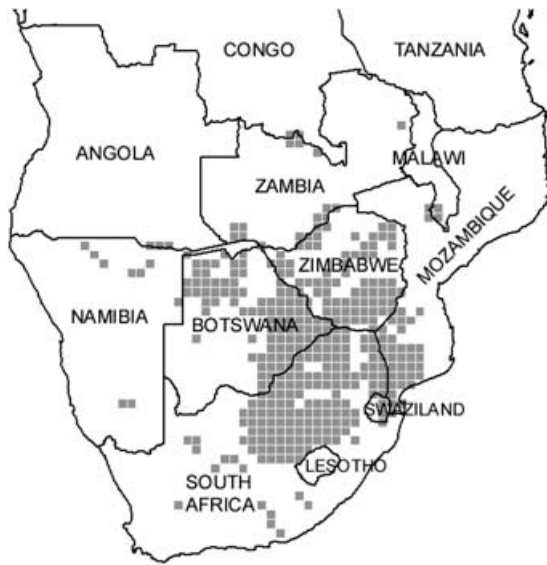


Fig. 3. Quarter-degree ($0.5^\circ \times 0.5^\circ$) grid squares where red-billed queleas have been recorded breeding in southern Africa between 1944 and 2005. Based on data with known coordinates and dates in the Natural Resources Institute archives (Venn *et al.* 1999) supplemented by unpublished information collected during the present study. Additional breeding localities (e.g. in Angola) based on data from 1836 onwards but which lack accurate date information or for which the resolution of the locations is too low for mapping at the 0.5° scale are given in Magor & Ward (1972).

of eggs, nestlings or fledglings was mentioned in the reports, however, this was used to calculate a more precise date when the colony was likely to have been founded, given that nest-building and egg-laying takes about 7 days, incubation 10 days, fledging 11–13 days (Ward 1965) and the post-fledging period is about 7 days.

Results

MODEL OUTPUT FOR 2002/2003

The model was consistent with events on the ground. Quelea breeding colonies were reported from 26 quarter-degree grid squares, of which only one (in Mozambique with two colonies) had received insufficient (≤ 300 mm) rainfall within the constraints of the model (> 240 mm within a 6-week span and at least 6 weeks elapsed after the 60-mm threshold had been exceeded) by the end of the season (Fig. 4a). Apart from the two Mozambique colonies, which were in an exceptional habitat (beside irrigated rice) and three colonies reported from south-east Zimbabwe in February (300 mm rainfall threshold criterion not met until after colonies were established), all the other 89 reported colonies (95%) were in zones indicated to have become suitable for breeding (Table 2).

MODEL OUTPUT FOR 2003/2004

Breeding was first possible in Angola and in South Africa south-east of Lesotho by mid-November (Fig. 2a).

A month later conditions were suitable for breeding in most of the eastern half of South Africa and parts of Angola, Botswana, Namibia, Zambia, Zimbabwe and Mozambique (Fig. 2b), by which time three colonies had been reported from South Africa. The first colonies in Botswana were reported on 2 February, heralding a season in which more than 100 colonies were found in that country with some still with young in nests as late as June (Jones *et al.*, in press).

Overall, 163 colonies were reported from 41 quarter-degree grid squares. Most (85%) colonies were in squares that the model had predicted to have become suitable (Table 2) but birds also bred in six grid squares that apparently received rainfall that did not meet the > 300 mm criterion by the end of the season (Fig. 4b). At the time of establishment, 25 colonies were in squares where ≤ 300 mm had fallen (five category G0, one G1, 18 G5 and one G7; Table 2), of which four were in Botswana and 21 in South Africa. All the latter were in the $27\text{--}28^\circ\text{S}$, $27\text{--}28^\circ\text{E}$ zone.

MODEL OUTPUT FOR 2004/2005

Unlike the previous season, 2004/2005 was characterized by a lack of any reports of quelea colonies in Botswana. There were few reports of breeding anywhere during 2004/2005, except in South Africa where 80 breeding colonies were located across 14 grid squares, 13 of which had received sufficient and appropriately timed rainfall and contained 79 (98.7%) of the 80 colonies (Fig. 4c, Table 2).

MODEL VALIDATION

The correspondence between model outputs and the locations of reported colonies was assessed with a null model in which the expected distribution of colonies among suitable and unsuitable grid squares was in proportion to the relative frequencies of squares in which sufficient or insufficient rain had fallen. Note that the squares from which the null expectations were calculated were restricted to those for which there are historical records of quelea breeding (Fig. 3). In two seasons, 2002/2003 and 2004/2005, colonies were reported significantly more often from squares in which sufficient rainfall had fallen within the model's time constraints (Fig. 4a,c: goodness-of-fit 2002/2003 $\chi^2 = 9.94$, $P = 0.0016$; 2004/2005 $\chi^2 = 7.63$, $P = 0.0057$). In 2003/2004, however, the distribution of reported colonies was not significantly different from the null model (Fig. 4b: $\chi^2 = 0.01$, $P < 0.99$).

For the colonies ($n = 337$), for which we had sufficient information to estimate the dates of their establishment to within 1 week, 85–99% occurred in grid squares where the > 300 mm criterion had been met (Table 2). No colonies were in squares where the 60 mm threshold had not been exceeded, but some (32) did occur where the > 300 mm requirement had not been achieved. Of these, 21 (66%) were

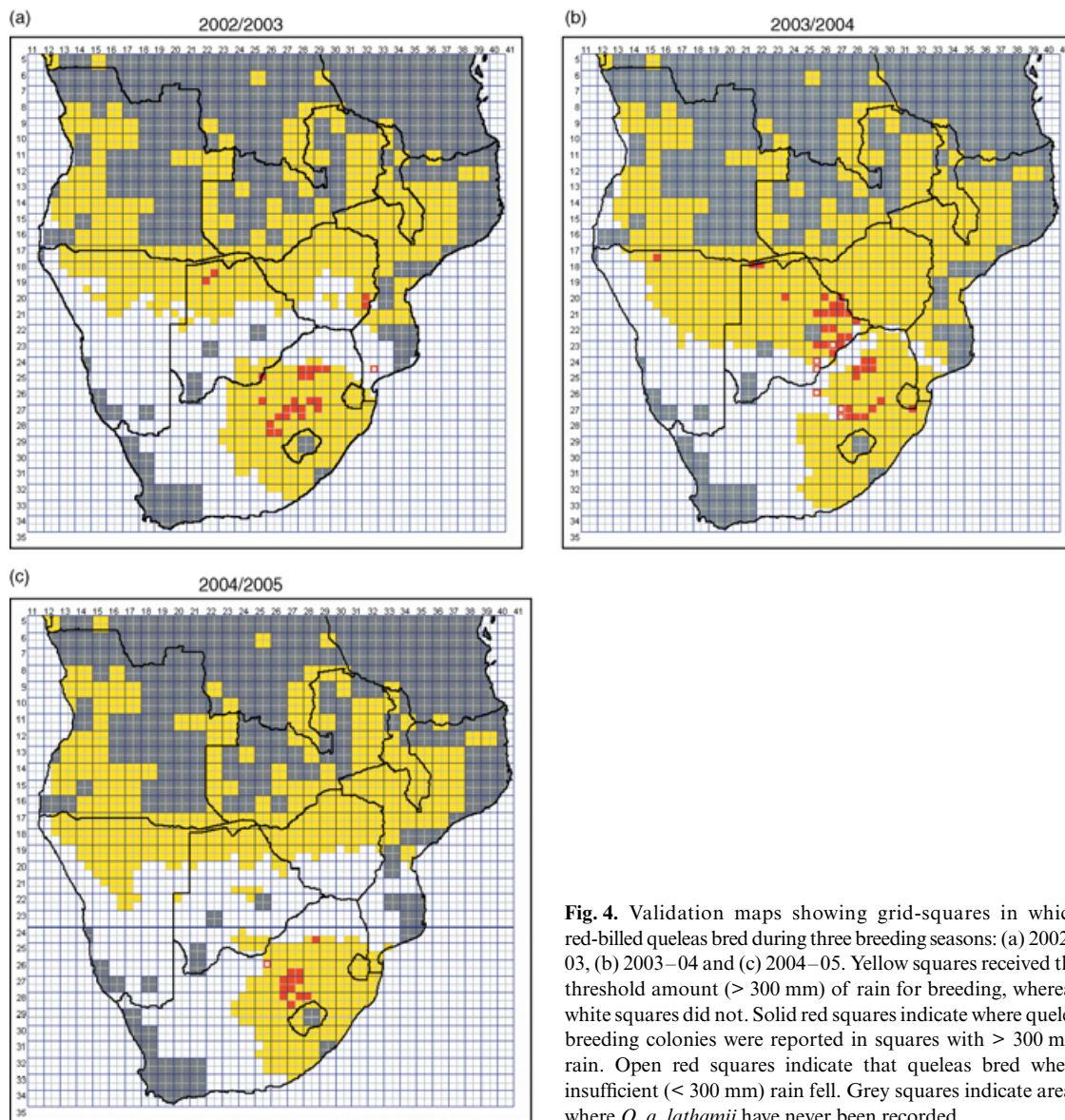


Fig. 4. Validation maps showing grid-squares in which red-billed queleas bred during three breeding seasons: (a) 2002–03, (b) 2003–04 and (c) 2004–05. Yellow squares received the threshold amount (> 300 mm) of rain for breeding, whereas white squares did not. Solid red squares indicate where quelea breeding colonies were reported in squares with > 300 mm rain. Open red squares indicate that queleas bred where insufficient (< 300 mm) rain fell. Grey squares indicate areas where *Q. q. lathamii* have never been recorded.

adjacent to at least one square where the criterion had been met.

For the smaller subset of colonies ($n = 51$) that were established with precisely known dates after achieving the > 300 mm requirement, 35% began within 2 weeks (Table 3). In some squares, however, breeding did not begin until up to 10 weeks later than we expected, suggesting that our assumptions about the speed with which habitats became unsuitable were too pessimistic.

Discussion

Using only rather crude assumptions about the threshold amounts of rain needed to trigger events in the breeding cycle of the red-billed quelea, we attempted to model the spatio-temporal distribution of breeding colonies in southern Africa in relation to rainfall estimates obtained by remote sensing. Despite its simplicity, the model performed well. In two of the three seasons for which the model was run, our results

differed significantly from the null expectation, i.e. breeding colonies were established almost exclusively in quarter-degree grid squares where sufficient rainfall (> 240 mm within a 6-week span and at least 6 weeks elapsed after the 60 mm threshold had been exceeded) had fallen by the end of the season. In a more refined analysis of a smaller subset of colonies for which precise dates of their establishment were known, their spatio-temporal distribution matched predictions in 95%, 85% and 99% of cases, respectively, over the three breeding seasons (Table 2), in line with the rainfall-migration hypothesis of Ward (1971).

Although the reported breeding colonies occurred overwhelmingly where the model estimated that conditions were suitable, many other such areas were not colonized. In many cases this may have been because existing colonies went unreported but in others birds may have been absent because they had already found suitable breeding conditions elsewhere. No colonies, however, were reported from regions where the first

Table 2. Analysis of amount of rainfall predicted by the model to have already fallen in the vicinity of breeding colonies at the time of their establishment in each of the three seasons 2002/2003, 2003/2004 and 2004/2005. Note that these totals refer only to colonies for which the establishment date could be estimated and are less than the total number of colonies reported. Column values indicate W = number of colonies established in quarter-degree grid squares ($0.5^\circ \times 0.5^\circ$) where the 60 mm threshold had not been passed (season not begun); G = where the 60 mm threshold, but not the 300-mm threshold, had been passed (season started, but not yet suitable for breeding). G0–8 indicate the number of surrounding squares where the 300-mm thresholds had been passed; R = squares where the 300 mm threshold had been passed (suitable for breeding); Y = as R but 6 weeks had elapsed since the 300-mm threshold was exceeded (presumed less suitable, see text)

	W	G0	G1	G2	G3	G4	G5	G6	G7	G8	R	Y	Total
2002/2003													
Botswana											1	4	5
Mozambique		2											2
South Africa											35	49	84
Zimbabwe		3											3
Total		5									36	53	94
% Red or yellow													94.7
2003/2004													
Botswana		2	1						1		30	70	104
Namibia												1	1
South Africa		3					18				6	30	57
Swaziland												1	1
Total		5	1				18		1		36	102	163
% Red or yellow													84.7
2004/2005													
South Africa					1						3	76	80
Total					1						3	76	80
% Red or yellow													98.7

Table 3. Number of colonies with precise establishment dates reported at different numbers of weeks elapsed since the model showed that the 300-mm rainfall threshold for breeding had been exceeded. Data for seasons 2002/2003, 2003/2004 and 2004/2005

Season	Weeks									
	1	2	3	4	5	6	7	8	9	10
2002/2003	2	2	3	4	2	0	0	4	3	1
2003/2004	7	4	0	0	0	1	0	2	4	0
2003/2005	2	1	0	1	5	3	0	0	0	0
Total	11	7	3	5	7	4	0	6	7	1
%	21.6	13.7	5.9	9.8	13.7	7.8	0	11.8	13.7	2

60 mm rainfall threshold had not been exceeded and in only a few instances did birds breed where the 300-mm threshold had not been passed. In one such case, at Chokwe in Mozambique in 2002/2003, queleas bred in association with a rice irrigation scheme where local conditions were evidently suitable despite a lack of adequate rainfall within an appropriate 6-week period.

In 2003/2004, 25 colonies were established where the 300-mm threshold had not been passed, but 21 of these were concentrated in the $27-28^\circ\text{S}$, $27-28^\circ\text{E}$ zone in South Africa, 18 of which were next to five squares that were suitable at the time of establishment. Similarly, a colony in Botswana was in a square surrounded by seven suitable squares. As a result of these 'near misses' and the presence of colonies in four apparently unsuitable squares in Botswana for 2003/2004, the overall distribution of reported breeding colonies did not differ significantly from the null model, with six of the 41 quarter-degree squares supporting colonies despite

apparently receiving insufficient rain. In such cases, the local conditions may have been better than the average indicated for the grid square, masked by an inevitable fuzziness introduced by using averages and by the operational needs to use weekly intervals in the algorithm definitions and to draw boundaries between squares. This consideration had led us to advise control teams that colonies could occur in apparently unsuitable squares if they were known to contain potential breeding areas and were next to squares that had received sufficient rainfall. Indeed, five of the six grid squares in question bordered squares where > 300 mm of rain was recorded within the appropriate time, and a corner of the sixth abutted one of these (Fig. 4b). All had received more than 188 mm of rain (range 189–240 mm) in at least one 6-week span within a minimum of 6 weeks of the 60 mm threshold being passed. The single colony recorded in 2004/2005 in a square where insufficient rain had fallen was also surrounded on three sides by squares that had received > 300 mm of

rain, satisfying the model criteria (Fig. 4c). Given the rather coarse (quarter-degree) resolution at which the pixel rainfall estimates were averaged, it may well have been that > 300 mm of rain did fall at the colony sites themselves but the threshold for the square as a whole was not exceeded, because of low rainfall values at other pixels within the square. We were also unable to take into account spatial differences in germination rates caused by soils differing in absorptency (Gaston 1973; Gaston & Lamarque 1976).

Although at least 85–99% of the colonies reported each season were at sites where sufficient rain had fallen, an unexpectedly high proportion of these were not established until a further 6 weeks had elapsed after the > 300 mm threshold criterion had been met. We had assumed that conditions become less suitable for breeding after this time because food resources diminish, and doubted that many colonies would be established so late in the local wet season but, in the event, the majority were in this category. For those with accurate data, 65% were established more than 2 weeks after we assumed the area had become less suitable (Table 3) and, in one case, as much as 10 weeks later. As it is unlikely that so many colonies could have been associated with very localized rainfall regimes different from the norm for their square, we conclude that habitats must remain suitable for quelea breeding much longer after the > 300 mm criterion has been met than previously realized. Therefore, in future modelling exercises it would be advisable to extend the period for which the squares remain suitable to at least 10 weeks and possibly for up to 12 weeks.

Our model may also be refined in other ways. Given that the amount of rainfall needed to stimulate grass seed germination may vary from 200 mm to as much as 450 mm according to soil type (Gaston 1973; Gaston & Lamarque 1976), further research should be directed at confirming such relations, so that thresholds may be adjusted spatially according to the soil types known to dominate in each grid square. Some inaccuracy in our forecasts may result from using the same algorithm to estimate rainfall for each grid square across the subcontinent. There are well-known limitations to the GOES Precipitation Index approach (Todd *et al.* 1995, 1999, 2001; Xu *et al.* 1999; Huffman *et al.* 2001), with rainfall estimates becoming less accurate the further south in southern Africa that they are used, the rainfall coefficient varying in space and time with variability in cloud microphysics. Indeed, a CTT threshold of -38°C , as used here, will identify only deep convective cloud systems and is likely to underestimate rainfall from processes such as shallow convection and orographic effects.

The present model runs for the entire breeding period without any input on the presence or absence of queleas in a grid square. While the model can predict with some accuracy where queleas will not breed it cannot predict in which grid squares queleas will breed, but only where they could do so. The model's predic-

tions could be greatly improved as the rainy season progresses by introducing Bayesian approaches to the algorithms, such as modifying the criteria if neighbouring squares have become suitable and/or by including updated information about quelea breeding activity from areas where their presence has already been confirmed (e.g. breeding still in progress or completed, colonies abandoned or control has taken place). These data may often be lacking, however, because in some countries field reporting systems are inefficient or non-existent, and information is inaccurate, slow to arrive or entirely absent. We are confident, however, that even in its present simple form and without real-time information on the activities of the birds themselves, this model is capable of providing useful forecasts. It shows, uniquely for any African bird species, where red-billed queleas most probably will not breed in a given year, and will enable quelea control teams to focus their attention on breeding areas most likely to be colonized by the birds if they are near to vulnerable croplands. This capability may be invaluable when allocating limited time and resources to control operations.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Combinations of parameter values used when calibrating the model.

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