

*Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Research Institute, Pretoria, South Africa, 24–26 March 1999.*  
*R. A. Cheke, L. J. Rosenberg and M. E. Kieser (eds) (2000) Natural Resources Institute, Chatham, UK.*

## 15 Quelea Populations and Forecasting in Southern Africa

P. J. Jones<sup>1</sup>, R. A. Cheke<sup>2</sup>, P. J. Mundy<sup>3</sup>, M. Dallimer<sup>1</sup> and J. F. Venn<sup>2</sup>

<sup>1</sup> Institute of Cell, Animal & Population Biology, University of Edinburgh, Edinburgh EH9 3JT, Scotland, UK (email: Peter.Jones@ed.ac.uk)

<sup>2</sup> Natural Resources Institute, University of Greenwich, Central Avenue, Chatham Maritime, Kent, ME4 4TB, UK

<sup>3</sup> Department of National Parks & Wild Life Management, PO Box 2283, Bulawayo, Zimbabwe

### ABSTRACT

Different subspecies of Red-billed Quelea, *Quelea quelea*, occur in different parts of Africa and each has its own migration pathways determined by local rainfall patterns and the availability of grass seed. The migration patterns of *Q. q. lathamii*, the subspecies present in southern Africa, began to be understood in the 1970s. Only now, however, are sufficient remote-sensed data on rainfall distribution and vegetation growth available over southern Africa as a whole to make the accurate prediction of quelea movements in any one year a realistic possibility. The DFID-funded project 'Models of quelea movements and improved control strategies' has assembled a computerised database of 3543 historical records of quelea occurrences throughout southern Africa, from which a forecasting model has been developed to assist pest managers in predicting control needs and targeting them effectively.

In parallel with this project, a DNA microsatellite study is being conducted to try to identify possible sub-populations of quelea within southern Africa and thereby assist in tracking their movements. Orientation studies on caged birds have also been carried out in Zimbabwe to establish the intended direction of movement during the 'early-rains migration', in order to detect whether a 'migratory divide' might separate birds heading towards two possible alternative destinations – Angola or South Africa – and hence lead to genetic differentiation. Preliminary results are discussed.

### INTRODUCTION

The overall strategy for the management of the Red-billed Quelea, *Quelea quelea*, now accepted Africa-wide, is to control only those birds likely to pose a threat to vulnerable local crops (Ward, 1979). The pattern of quelea occurrences, however, is very variable from year to year, depending on regional variations in rainfall and grass seed production. In addition, the reporting of quelea occurrences, whether as roosts or breeding colonies, is often haphazard and slow, such that national control teams may find it difficult to mobilise in time or to operate with full efficiency and effectiveness. What is required is a forecasting system for quelea similar to that already existing for African Armyworm, *Spodoptera*

*exempta*, which can almost instantaneously incorporate remotely-sensed data on relevant environmental parameters into a simple predictive model that can be used in the field (Holt *et al.*, 2000 or see page 151).

This paper reports on the project ‘Models of Quelea Movements and Improved Control Strategies’, funded by the UK Department for International Development (DFID) and being carried out on the southern African race of the Red-billed Quelea, *Q. q. lathamii*. It also reports on work, collaborative with this project, on molecular genetic variation in Red-billed Quelea, as part of a CASE studentship to Edinburgh University and the Natural Resources Institute (NRI) funded by the UK Natural Environment Research Council. The DFID project is centred on Zimbabwe, where the target institutions are the Ornithological Research Unit and the Problem Bird Control Unit of the Department of National Parks and Wild Life Management. It also involves the collection of additional data from the surrounding countries of the Southern African Development Community (SADC) that share the same quelea populations.

In order to achieve the prime objective of building a practical quelea forecasting model, these two parallel projects have involved three main areas of work.

- (1) The compilation of an electronic database of historical quelea records in SADC countries (but excluding Tanzania, which harbours only the separate East African subspecies, *Q. q. intermedia*).
- (2) A re-assessment of the conjectured migration patterns of Red-billed Quelea in southern Africa, as originally proposed by Ward (1971) and Jones (1989b). This is based on new information from plumage polymorphisms and patterns of molecular genetic variation using microsatellite DNA to identify and track discrete sub-populations during their annual migrations, and from an investigation of the preferred migratory orientation of birds preparing for the ‘early-rains migration’. This work is also attempting to resolve the ‘*spoliator* problem’ – the uncertainty surrounding the possible existence of a genetically discrete second population of quelea in southern Africa (Jones *et al.*, 1998, 2000), which would have implications for quelea management.
- (3) The construction of the computer model itself.

## THE NRI QUELEA DATABASE

An electronic database has been re-compiled from the Quelea Archives originally assembled by Joyce Magor (Magor and Ward, 1972; COPR, unpubl.) in the early 1970s at the former Centre for Overseas Pest Research (COPR, now NRI). The original electronic database on magnetic tape was lost but one hard copy of the print-out was preserved. It was from this that 3543 separate entries concerning SADC countries have been re-keyed by Nicola Buss into an Access database at NRI (Venn *et al.*, 1999).

In its current state, the database extends from 1836 (South Africa) to 1974 but subsequent years up to the present (with inevitable gaps for some countries) are being added from Botswana, Namibia, South Africa and Zimbabwe, including raw data from the Southern African Bird Atlas Project (Harrison *et al.*, 1997). The most useful information is available only from the early 1950s, detailing precisely located colonies where the dates of egg-laying are known (these form the basis of the predictive model – see below) but the database also contains details of dry-season roosts, control operations, and reported crop damage.

## A RE-ASSESSMENT OF QUELEA MIGRATION STRATEGIES IN SOUTHERN AFRICA

The migration patterns and the timing of the annual cycle (breeding, moult, etc.) of Red-billed Quelea are all determined by seasonal changes in food availability (annual grass seeds, insects) and hence, ultimately, by the movements of local rain-fronts (Ward, 1971; Jones, 1989a). A general model of quelea migrations in southern Africa was first described in detail by Jones (1989b) and it is this that forms the basis of the predictive model being developed by the NRI project (see below). However, two aspects of quelea biology that were highlighted by Jones's (1989b) review remain unresolved – flock cohesion and the 'spoliator problem'. Their resolution will greatly improve our understanding of how quelea population structure relates to their migration patterns, thereby providing a stronger theoretical framework to support the assumptions of the forecasting model.

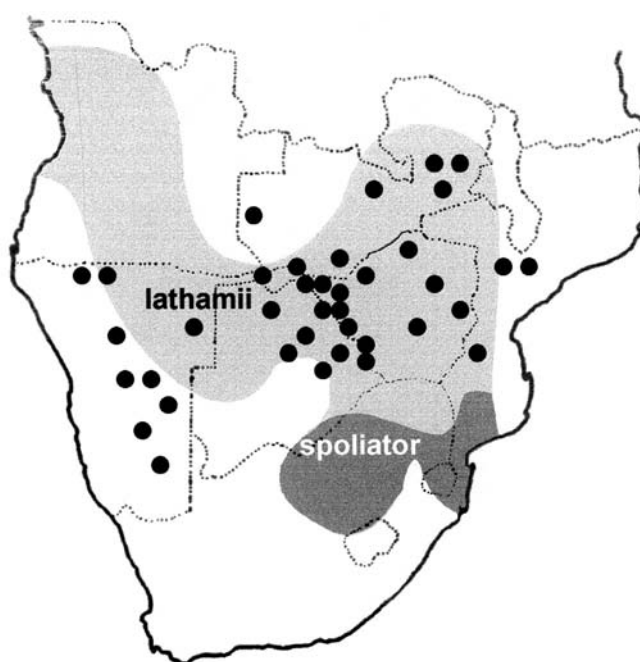
### Flock Cohesion and Genetic Variation at the Sub-Population Level

Several lines of evidence indicate that quelea aggregations may be remarkably cohesive over long distances and prolonged periods, which may include the breeding season (Jaeger *et al.*, 1986, 1989; Jones, 1989b). M. Jaeger (*in litt.*) has suggested theoretical reasons why such cohesion might be adaptive in the context of the Red-billed Quelea's wide-ranging migration and nomadism. We suspect that such cohesion within aggregations, which rarely mix, might account for differences occasionally observed between the plumage characters of males in adjacent breeding colonies (P. J. Jones, unpubl.). The extensive DNA sampling being carried out by M. Dallimer will provide molecular genetic data to establish whether the Red-billed Quelea forms a homogeneous and freely-interbreeding population across southern Africa, or whether it is subdivided into genetically distinct sub-populations maintained by differences in geographical range, migration patterns or seasonality of breeding.

Seventy-three avian microsatellite primers from 16 species in eight families have been tested for cross-species amplification using Red-billed Quelea DNA as a template, obtained from blood samples collected in Bulawayo, Zimbabwe in 1997. Twenty-one markers from nine species successfully amplified an homologous product, with some loci proving to be highly polymorphic (Dallimer, 1999). Six out of eight markers from the most closely-related species, the White-browed Sparrow-weaver *Plocepasser mahali*, worked. The extensive sampling programme is still in progress and has involved obtaining series of blood samples from many hundreds of birds collected in Botswana, Namibia, South Africa and Zimbabwe. In most cases these derive from breeding colonies at each of which 50–80 males and *c.* 20 females were sampled and full plumage data recorded for each bird. The data are currently being analysed.

### The Validity of *Q. q. spoliator*

The other unresolved issue raised by Jones's (1989b) review was the taxonomic validity of a second putative subspecies of Red-billed Quelea, *Q. q. spoliator*, within southern Africa, where previously *Q. q. lathamii* had been the only subspecies recognised from the region. *Q. q. spoliator* was described from KwaZulu-Natal by Clancey (1960), and was claimed to be typical of quelea breeding in the wetter areas of the central highveld and eastern coastal zone of South Africa, Swaziland and southern Moambique (Figure 1), i.e. the south-eastern part of the formerly-accepted range of *Q. q. lathamii*. Subsequent work by Clancey (1968, 1973) suggested that *spoliator* occurs during the non-breeding season (May to November) throughout the interior of southern Africa, including Namibia, within the breeding range of *Q. q. lathamii* (Figure 1). A clear resolution of the taxonomic distinctness of these two



**Figure 1** Conjectured breeding distributions of *Q. q. lathamii* (light grey shading) and *Q. q. spoliator* (dark grey shading). Filled circles indicate occurrences during the non-breeding season (May to November) of *spoliator*-type individuals within the breeding range of *lathamii* (after Clancey, 1973).

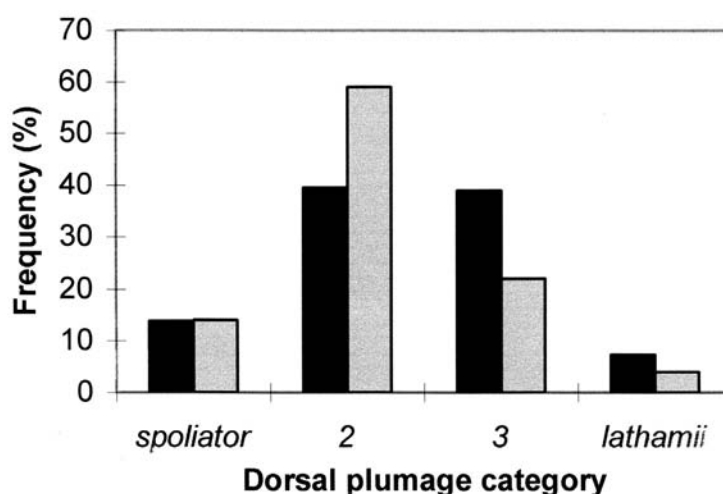
subspecies is required if the migratory behaviour of southern African quelea is to be properly understood and lead to a more effective control strategy.

The validity of *Q. q. spoliator* is particularly difficult to assess, because it was described on the basis of differences in the colour of the upper-parts in non-breeding plumage (grey-brown in the case of *Q. q. spoliator*, compared to the warm buff-brown of 'true' *Q. q. lathamii*). In contrast, all other subspecies of the Red-billed Quelea had been characterised by the different plumage morphs of males in breeding dress (Ward, 1966). These differences can be reliably quantified only in large, randomly-sampled collections of breeding males (Ward, 1966, 1973; Jaeger *et al.*, 1989), which has still not been done for birds within the *Q. q. spoliator* breeding range.

The taxonomic status of *Q. q. spoliator* has remained controversial for two further reasons: (a) intermediates between *Q. q. spoliator* and *Q. q. lathamii* occur throughout southern Africa (Lourens, 1961), and even museum specimens designated as *Q. q. spoliator* by Clancey himself show wide variation in dorsal coloration (Jones *et al.*, 1998, 2000); and (b) both *Q. q. lathamii* and *Q. q. spoliator* must respond in similar ways to the timing and distribution of rainfall, such that they remain sympatric for much of the year and, most crucially, when they are breeding (Jones, 1989b).

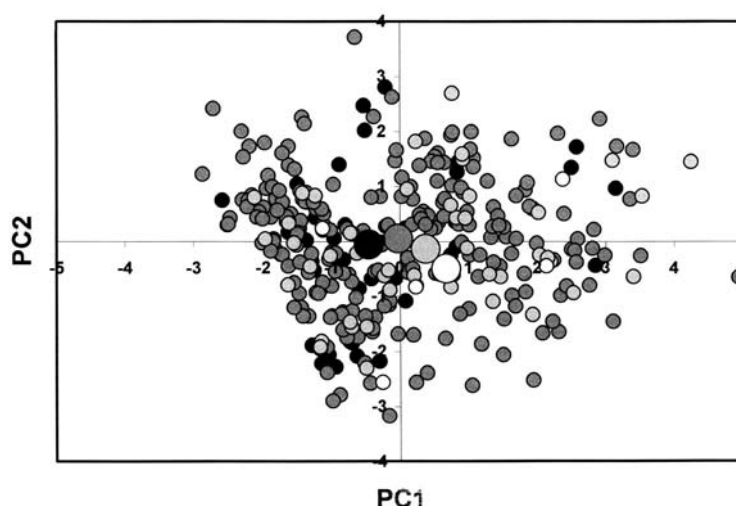
We therefore collected new plumage data to distinguish *spoliator* from *lathamii*, and data on the timing of prenuptial moult and gonadal growth to establish whether possible differences in the timing of breeding, resulting from differing migration patterns, could maintain genetic isolation between them (Jones *et al.*, 1998).

Based on comparison with the dorsal coloration of museum specimens, males from breeding colonies in Zimbabwe in March 1998 were scored as *spoliator*, *lathamii*, or intermediate,



**Figure 2** Frequency distributions of *spoliator*-type, *lathamii*-type, and intermediate Red-billed Quelea, based on dorsal plumage coloration. Black bars: birds in non-breeding plumage (no difference between males and females, sexes therefore combined,  $n = 230$ ); grey bars: breeding males only ( $n = 99$ ).

and their breeding plumage morphs were recorded. These data showed that the whole range of dorsal coloration, from *spoliator* to *lathamii*, was represented among males in the same breeding colonies well within the supposed breeding range of *Q. q. lathamii* (Figure 2). These same males were also scored for the polymorphisms in their breeding plumage to see whether there was any association between morph frequencies and dorsal coloration. A Principal Components Analysis of these data showed no discrete clusters of individuals associated with the prior classification into *spoliator*- or *lathamii*-type and that the category means are indistinguishable from each other in the centre of the distribution (Figure 3).



**Figure 3** A Principal Component scatter-plot of plumage variation among breeding male Red-billed Quelea that had been independently scored as 1 (black circles) = *spoliator*-type, 2 and 3 (dark grey and light grey) = intermediate, 4 (open circles) = *lathamii*-type on the basis of their dorsal plumage coloration. PC1 + PC2 represents nearly 50% of variation in male plumage pattern. A positive PC1 indicates a pinker, more deeply coloured belly and lesser extent of grey, scaly feathers on the chest. A higher PC2 score indicates a greater width of the black facial mask above and below the beak. Large symbols indicate the means of each distribution.

Although further extensive data on plumage polymorphisms from across southern Africa are still being analysed, in conjunction with the DNA microsatellite study (M. Dallimer, unpubl.), on the basis of present evidence we have come to the preliminary conclusion that, because '*spoliator*' individuals cannot be separated from *lathamii* on morphological criteria in either breeding or non-breeding plumage, and because all colour variants breed in the same places at the same time, the subspecies *Q. q. spoliator* does not reflect any significant phylogenetic division.

### **The 'Early-Rains Migration' and a possible 'Migratory Divide'**

One further mechanism remains unexplored, however, by which two genetically distinct populations might co-exist within southern Africa. Jones (1989b) did not consider in this context Ward's (1971) suggestion that quelea might migrate in different directions at the start of the rains and so become separated into two sub-populations. As described in greater detail below, virtually all Red-billed Quelea leave the interior of southern Africa each year by late November, when the remaining dry grass seed germinates. They must then perform an 'early-rains migration' to parts of southern Africa where the rains had begun earlier and where fresh grass seed is by now available. There are two possible destinations offering such conditions: Clancey's suggested *spoliator* breeding range in South Africa and Mozambique or, alternatively, Angola to the north-west, where the rains also begin in September-October (Ward, 1971; Jones, 1989b). There is no information on the relative proportions of the population that might fly in either direction. It is possible that were such a separation then to persist during the first breeding attempt of the wet season, some degree of genetic isolation between the sub-populations might be established. A migratory divide of this sort could therefore separate *spoliator*, flying to early-rains quarters in the south-east, from *lathamii* flying north-west.

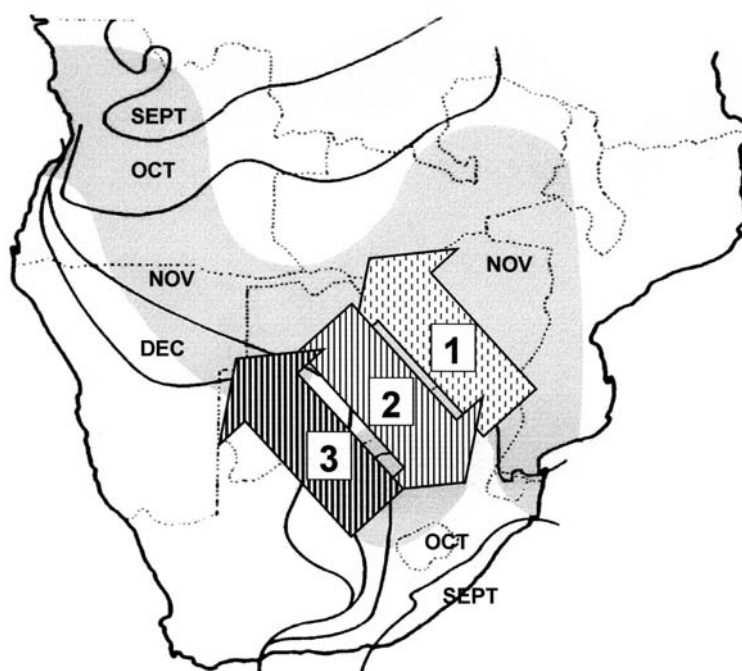
Such a possibility had not previously been considered but is now being investigated further. The preferred migratory directions of quelea have been measured in orientation cages using birds caught during the period of rapid pre-migratory fattening in Zimbabwe in November 1998. All birds were blood-sampled and their plumage morphs recorded; these data are still being analysed (M. Dallimer, unpubl.).

## **THE NRI FORECASTING MODEL**

### **Biological Background**

In southern Africa much of the loss to subsistence agriculture caused by quelea involves damage to rain-fed sorghum and millet at the milky-doughy stage shortly before harvest. The damage is almost always caused by newly-independent juveniles from nearby breeding colonies, usually within a 10–30 km radius. In contrast, the adults at breeding colonies tend not to be a major problem, because during colony establishment, egg-laying, incubation, and the nestling period, their diet consists almost exclusively of insects and wild grass seeds (Ward, 1965; Jones, 1989c). Furthermore, they abandon their young at fledging and seek new breeding sites elsewhere, often hundreds of kilometres away.

After breeding has finished, the former colony may then serve as a roost for a further 1–2 months for these juveniles, which may be joined by others born earlier in distant colonies whose local food supplies have become exhausted. Such roosts in favourable areas may continue to attract increasing numbers of young birds and, eventually, post-breeding adult quelea, and may persist well into the ensuing dry season, though by then all local subsistence crops have long been harvested. It is only in areas where irrigated wheat is grown commercially in the dry season that such aggregations may be problematic.



**Figure 4** Schematic representation of Red-billed Quelea migration patterns in southern Africa. Arrow 1: birds forced ahead of the rain-front as rains begin in the areas of earliest rainfall; arrow 2: all birds perform an 'early-rains migration' over the advancing rain-front; arrow 3: birds return to areas of successively later rainfall on 'breeding migration'. For simplicity, this scenario does not illustrate any 'migratory divide' (see text). The grey shaded area indicates the approximate breeding range of both *lathamii* and '*spoliator*' combined. Isohyets indicate the start of the wet season.

Because this project is concerned only with alleviating damage to rain-fed subsistence crops, our model is intended to forecast the timing and locations of quelea breeding colonies that would require control to prevent successful fledging of juveniles. We are not concerned here with the forecasting of damage to commercially grown irrigated cereals.

The forecasting model developed by the NRI project is, therefore, designed to predict where and when breeding colonies will be established. Then pre-emptive control can protect local cereal crops that will mature some 5 weeks later, when the newly-fledged and inexperienced juveniles are abandoned by their parents and left to fend for themselves.

The basis of the NRI model is the conjectured migration pattern of quelea in southern Africa first proposed by Ward (1971) and developed by Jones (1989b), in which the timing and distribution of rainfall and the growth of annual grasses are the main determinants of the birds' movements. As shown schematically in Figure 4, when the rains begin in the first areas to receive rainfall and grass seed germinates, quelea are forced ahead of the rain-front to the remaining dry areas where un-germinated seed remains. By November, grass seed germinates everywhere across the birds' range in the interior of southern Africa. This sudden lack of food forces quelea to move once more, and they perform an 'early-rains migration' back across the rain-front to the first areas to have received rain. Here, by now, fresh seed and the insect prey required for breeding (mainly caterpillars and nymphal grasshoppers) are available in large quantities, providing conditions suitable for the first breeding attempt of the season. Although it is still unresolved whether a 'migratory divide' splits the southern African quelea population into two sub-populations, one heading for areas of early rain in north-west Angola and the other to Mozambique and South Africa

(not shown in Figure 4; see above), this does not fundamentally affect the structure of the model. Its resolution, however, will improve the model's predictions.

On arrival in the early-rainfall areas, some birds breed immediately, while others come into condition more slowly and begin breeding somewhat 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 also now becoming available. Somewhere along the route of this breeding migration, birds will breed wherever suitable conditions of rainfall and grass growth have occurred, and avoiding areas of drought. Because some places may reliably provide good breeding conditions for quelea in most years, even under a variable rainfall regime, these may represent traditional breeding sites to which birds return year after year. Other areas may be occupied only if the traditional sites prove unsuitable, or otherwise only in years of above-average rainfall. Even then, they may remain unoccupied if the birds have settled elsewhere first.

### Structure of the Model

Like the armyworm model described in these proceedings (Holt *et al.*, 2000; see page 151), the quelea forecasting model is rule-based, allowing qualitative data to be used and incorporating state changes by logical 'if-then' type rules. Areas (grid-squares) become suitable for breeding after a gap of at least 6–8 weeks following grass seed germination and after a minimum amount of rain has fallen to produce new seed (and insects) in sufficient quantity. Quelea may then breed in the grid-square provided there are not equally suitable areas already fulfilling these conditions available in the direction of the early-rains migration, i.e. in the early-rains quarters. If there are, then breeding birds will be occupied there for the duration of a breeding attempt (5 weeks + 1 further week to regain breeding condition) before they can move elsewhere, though this period may be shorter if the breeding attempt is already partly completed. Only after earlier breeding attempts are completed can birds occupy grid-squares of later rainfall but, even then, because breeding conditions are ephemeral and the opportune time in any one place is very short, 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 quelea and, by this time, caterpillars and nymphal grasshoppers have become adults and are unavailable as prey. Quelea seeking new nesting areas will by-pass such places and move on further along the line of the breeding migration to areas of even later rainfall. Such a leap-frogging process will continue until no more areas are suitable to receive birds that are ready to make a further breeding attempt, and the breeding season comes to an end.

To construct the quelea forecasting model, the timing and amount of rainfall necessary to initiate breeding have been established from correlations between past rainfall records and the dates of breeding attempts in the quelea database. For breeding records since 1981 it has also been possible to establish how the growth condition of local vegetation correlates with quelea breeding attempts, using the NOAA-AVHRR Normalised Difference Vegetation Index (NDVI) data as a measure of vegetative productivity (FAO, 1991).

The model's resolution is specified by one-degree grid-squares (*c.* 11,500 km<sup>2</sup> at these latitudes) and 10-day periods. It may be possible (and much more useful) to improve the spatial resolution to 30' × 30' squares (*c.* 2860 km<sup>2</sup>), since the distribution of suitable quelea breeding sites is patchy and generally confined to distinctive vegetation types (*Dichrostachys-Acacia* bush, mainly *A. mellifera*, and occasionally reedbeds). The relevant data are being obtained from detailed vegetation maps where available. The temporal resolution is



currently constrained by imprecision in the recording of laying dates in the historical database but, in any case, it may be conveniently taken to correspond with the 10-day resolution of the NDVI data.

To run the model, all that is required is to enter rainfall estimates obtained from Meteosat Cold Cloud Duration (CCD) data and the corresponding NDVI values. Confirmation of the presence or absence of quelea is not initially needed and, indeed, the model can run for the entire breeding period without such input, though its predictions become less useful. Of course, the precision of the model is greatly improved as the rainy season progresses 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.

The prototype model is still being developed and its predictions tested against field observations.

## ACKNOWLEDGEMENTS

This document is an output from a project funded through the Crop Protection Programme of the UK Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. Project R6823, Crop Protection Programme.

For help with the fieldwork and data collection, we wish to thank: *in Botswana*: Remi and Wendy Borello, Rebecca Kolare, K. C. Mathafeni, Kekopamane Mbwe, T. S. Moruti, P. O. P. Mosupi, T. Onalenna, R. Seatla, and K. Zambo; *in Namibia*: Abisai Aipanda, Monica Andreas, Phoebe Barnard, Chris Brown, Colin Craig, S. T. Ekandjo, Alice Jarvis, Sue McRae, John Mendelson, Caroline Roberts, Tony Robertson, Harry and Hannah Schneider, Rob Simmons and Berthold Wohlleber; *in South Africa*: Adrian Craig, Luka Geertsema, James Harrison, Peter Martinez, Dieter Oschadleus, Les Underhill, Etienne van der Walt and Craig Whittington-Jones; *in Zimbabwe*: Ngoni Chiweshe, Tracey Couto, Bruce Davison, James Dale, Derek de la Harpe, Ron Hartley, Michael Irwin, Douglas Kabale, Albert Kumirai, Cecil Machena, Shilla Machiri, Boniface Magwisi, Audrey Msimanga, Dorothy Nyamhanza, Chris Pakenham, John Paxton, Headman Sibanda, F. Z. Sithole, Clive Stockil, Takawira Temba and Leonard Ungani. For providing the microsatellite primers used in this study we also thank S. Bensch, H. Cheng, M. Double, A. Fridolfson, A. Johnson, S. McRae, J. Pearce, S. Piertney and J. Wetton.

## REFERENCES

- CLANCEY, P. A. (1960) A new race of Red-billed Quelea from south-eastern Africa. *Bulletin of the British Ornithologists' Club* **80**: 67–68.
- CLANCEY, P. A. (1968) Subspeciation in some birds from Rhodesia II. *Durban Museum Novitates* **8**: 153–182.
- CLANCEY, P. A. (1973) The subspecies of the *lathamii*-group of *Quelea quelea* (Linnaeus). *Durban Museum Novitates* **10**: 13–22.

DALLIMER, M. (1999) Cross-species amplification of microsatellites in passerines. *Molecular Ecology* **8**: 695–698.

FAO (1991) *FAO-ARTEMIS NOAA AVHRR NDVI Image Bank Africa 1981–1991*. Food and Agriculture Organisation of the United Nations, Rome, Italy.

HARRISON, J. A., ALLAN, D. G., UNDERHILL, L. G., HERREMANS, M., TREE, A. J., PARKER, V. and BROWN, C. J. (eds) (1997) *The Atlas of Southern African Birds*. BirdLife South Africa, Johannesburg, RSA.

HOLT, J., MUSHOBOZI, W. L., TUCKER, M. L. and VENN, J. F. (2000) Modelling armyworm population dynamics to forecast outbreaks. pp 151–163. In: *Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Research Institute, Pretoria, 24–26 March 1999*. CHEKE, R. A., ROSENBERG, L. J. and KIESER, M. E. (eds). Natural Resources Institute, Chatham, UK.

JAEGER, M. M., BRUGGERS, R. L., JOHNS, B. E. and ERICKSON, W. A. (1986) Evidence of itinerant breeding of the red-billed quelea *Quelea quelea* in the Ethiopian Rift Valley. *Ibis* **128**: 469–482.

JAEGER, M. M., ELLIOTT, C. C. H., BRUGGERS, R. L. and ALLAN, R. G. (1989) Distribution, populations and migration patterns of Quelea in eastern Africa. pp. 113–131. In: *Quelea quelea: Africa's Bird Pest*. BRUGGERS, R. L. and ELLIOTT, C. C. H. (eds) Oxford University Press, Oxford, UK.

JONES, P. J. (1989a) General aspects of Quelea migrations. pp. 102–112. In: *Quelea quelea: Africa's Bird Pest*. BRUGGERS, R. L. and ELLIOTT, C. C. H. (eds). Oxford University Press, Oxford, UK.

JONES, P. J. (1989b) Distribution, populations and migration patterns of Quelea in southern Africa. pp. 132–143. In: *Quelea quelea: Africa's Bird Pest*. BRUGGERS, R. and ELLIOTT, C. C. H. (eds). Oxford University Press, Oxford, UK.

JONES, P. J. (1989c) Factors determining the breeding season and clutch size. pp. 158–180. In: *Quelea quelea: Africa's Bird Pest*. BRUGGERS, R. L. and ELLIOTT, C. C. H. (eds). Oxford University Press, Oxford, UK.

JONES, P. J., CHEKE, R. A. and MUNDY, P. J. (1998) Migration patterns of Red-billed Queleas *Quelea quelea* in southern Africa and the validity of *Q. q. spoliator*. In: *Proceedings. 22nd International Ornithological Congress, Durban*. ADAMS, N. J. and SLOTOW, R. H. (eds). *Ostrich* **69**: 402–403.

JONES, P. J., DALLIMER, M., CHEKE, R. A. and MUNDY, P. J. (2000) Are there two subspecies of Redbilled Quelea *quelea quelea* in southern Africa? *Ostrich* (in press).

LOURENS, D.C. (1961) Comments on the new race of the Red-billed Quelea. *Ostrich* **32**: 187.

MAGOR, J. and WARD, P. (1972) Illustrated descriptions, distribution maps and bibliography of the species of *Quelea* (weaver-birds: Ploceidae). *Tropical Pest Bulletin* **1**: 1–23.

VENN, J. F., CHEKE, R. A. and JONES, P. J. (1999) *Quelea Bird-pest Database: Southern Africa Data*. Natural Resources Institute, Chatham, UK.

WARD, P. (1965) Feeding ecology of the Black-faced Dioch *Quelea quelea* in Nigeria. *Ibis* **107**: 173–214.

WARD, P. (1966) Distribution, systematics, and polymorphism of the African weaver-bird *Quelea quelea*. *Ibis* **108**: 34–40.

WARD, P. (1971) The migration patterns of *Quelea quelea* in Africa. *Ibis* **113**: 275–297.

WARD, P. (1973) *Manual of Techniques used in Research on Quelea Birds*. AGP:RAF/67/087 Working paper. UNDP/FAO, Rome, Italy.

WARD, P. (1979) Rational strategies for the control of queleas and other migrant pest birds in Africa. *Philosophical Transactions of the Royal Society of London B* **287**: 289–300.