

S31-2 Bird population explosions in agroecosystems — the quelea, *Quelea quelea*, case history

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Abstract There is some evidence to suggest that the quelea, probably the world's most numerous bird, has existed for centuries in enormous populations in sub-Saharan Africa, subsisting mainly on the seeds of annual grasses in semi-arid savannas. Large populations occur because their staple food is abundant and because they can move opportunistically to areas that have received good rain and breed. The quelea is a highly visible pest of small-grain cereal crops: wheat, rice, sorghum and millet. Farmers often perceive quelea as more of a menace than it really is. Farmers also claim that quelea populations are increasing at the expense of their crops, but seldom have supporting evidence. The few quelea population estimates that have been made have not been repeated or tested for accuracy, and it is thus difficult to establish trends. Indirect population information includes atlasing and government records of the numbers killed in control operations. Distribution data suggest that drought can be a major factor in limiting distribution. There is, however, evidence for range expansion in South Africa, but the reasons for it are uncertain and do not necessarily imply population increase. Data from control kills show fluctuations but no consistent upward trend. A review of the changes in African agro-ecosystems in relation to their possible influence on quelea populations suggests that natural food sources in regional savannas still greatly exceed the food available from an agriculture that is dominated by maize, a crop not eaten by quelea. In the next few decades, quelea population levels are likely to continue to be controlled by rainfall/wild grass seed production in their breeding habitats. In the longer term, human population expansion and cutting of acacia bush for charcoal could affect those populations negatively.

Key words Quelea, Bird populations, Agro-ecosystem changes

1 Introduction

The red-billed quelea (*Quelea quelea*) is a prime example of a gregarious bird adapted to semi-arid habitats that has a significant impact on agriculture. It occurs exclusively in sub-Saharan Africa, typically in *Acacia* savannas where it sometimes gathers in vast flocks of several million, and where it breeds gregariously in colonies that sometimes cover more than 100 ha and include about 30 000 nests per hectare. It is thought to be the most numerous bird in the world, totaling about 1 500 million at the end of the breeding season (Elliott, 1989). The enormous populations of quelea are generally thought to occur for two main reasons. First, their staple diet of wild annual grass seed, given sufficient rain, is abundant but patchily distributed over extensive semi-arid habitats. Gaston (1976) showed that over 2t/ha could be produced in natural quelea habitat with an annual rainfall of about 450 mm. Secondly, the ability of quelea to follow movements of the Inter-tropical Convergence Zone, and consequent rainfall, allows them to breed itinerantly two or three times per year wherever conditions are most favorable (Ward, 1971; Jaeger et al., 1986; Elliott, 1990).

In the context of bird population explosions in agroecosystems, this paper will review the evidence for popula-

tion explosion in quelea and, where there is evidence of population change, consider the factors that may have been involved.

2 Quelea as an agricultural pest

Because the quelea is an agricultural pest, official statements are often made that its populations are increasing, or are causing serious damage to crops, or are becoming permanently resident in agricultural areas. Such reports may be made to induce a sense of urgency or to encourage national treasuries or donors to fund quelea control. The statements are also sometimes repeated in scientific publications, but usually without supporting data (Mundy and Herremans, 1997). Obtaining supporting data is laborious and costly. Quelea can and regularly do cause severe damage locally to crops, and objective data exist in which the levels of losses have been measured (Jaeger and Erickson, 1980; Elliott, 1989). The high visibility of quelea flocks, and the fact that most quelea control involves the aerial spraying of pesticides at Government cost, often encourages farmers to exaggerate their problems. On the other hand, farmers have to scare the birds from their fields all day long during the period covering the crop's milky stage to harvest. This is a demanding task for a smallholder and an expensive activity for large farms. Because quelea are there when crops

are ripe, farmers assume they are resident. Such perceptions should be treated with scepticism except when properly substantiated

Serious quelea damage to crops is not a recent phenomenon. One of the earliest records is of a famine in Central Tanzania in 1881 (Brooke, 1967), attributed at least in part to quelea. Maize was introduced by the Portuguese in West Africa in the 16th century and probably in East Africa in the 17th century. It apparently became a staple crop partly because of its resistance to bird damage (Miracle, 1965; Reader, 1998). This implies that quelea was also a pest in those times as it cannot peel the maize cob. Great flocks of quelea are supposed to have existed for centuries; nor is there any reason to suppose that their staple food, wild grass seed (Ward, 1965; Erickson, 1989), has been in short supply during the last few hundred years, except during widespread droughts. Quelea were recorded in 1836 in southern Africa (Layard, 1867; Whittington-Jones, 1997), but their association with agricultural damage was only mentioned in the early 1900s (Johnston, 1907; Schlupp, 1922; Whittington-Jones, 1997). Large flocks of quelea were first reported in the Sudan in 1914 by the naturalist Abel Chapman (C.E. Wilson, pers. comm.) who noted the potential threat to agriculture. Following increasing numbers of complaints by farmers in South Africa, Government intervention to control quelea began in 1952 (Whittington-Jones, 1997).

3 Estimates of quelea populations

To my knowledge, only South Africa and Zimbabwe systematically collect and estimate the numbers of quelea killed during control operations. In Tanzania, indirect estimates were made during the 1980s, but this practice no longer continues. In the other 14 countries in which quelea are controlled, figures given are not reliable as the teams have a vested interest in maximizing reports. Crook and Ward (1968), while describing the numbers reported killed as "fantastic", concluded that the total quelea population might lie between 1 000 million and 100 000 million. Elliott (1989) attempted to estimate regional populations by reviewing information on the breeding distribution and the number of breeding colonies found using a helicopter, the most efficient means of locating colonies. From the number of colonies found and an estimate of the percentage of the potential breeding area actually searched, an estimate was made of the total number of breeding colonies present and hence the total breeding population. The post-breeding population was assumed to be double that figure, i.e. 1 500 million, based on a survival rate of 2.2 fledglings per nest (Jones, 1989b), indicating that the quelea is the most numerous bird in the world.

The detailed results suggested that there was a post-breeding population of 124 million in Tanzania, 534 million in the Sudan, and about 380 million in southern Africa.

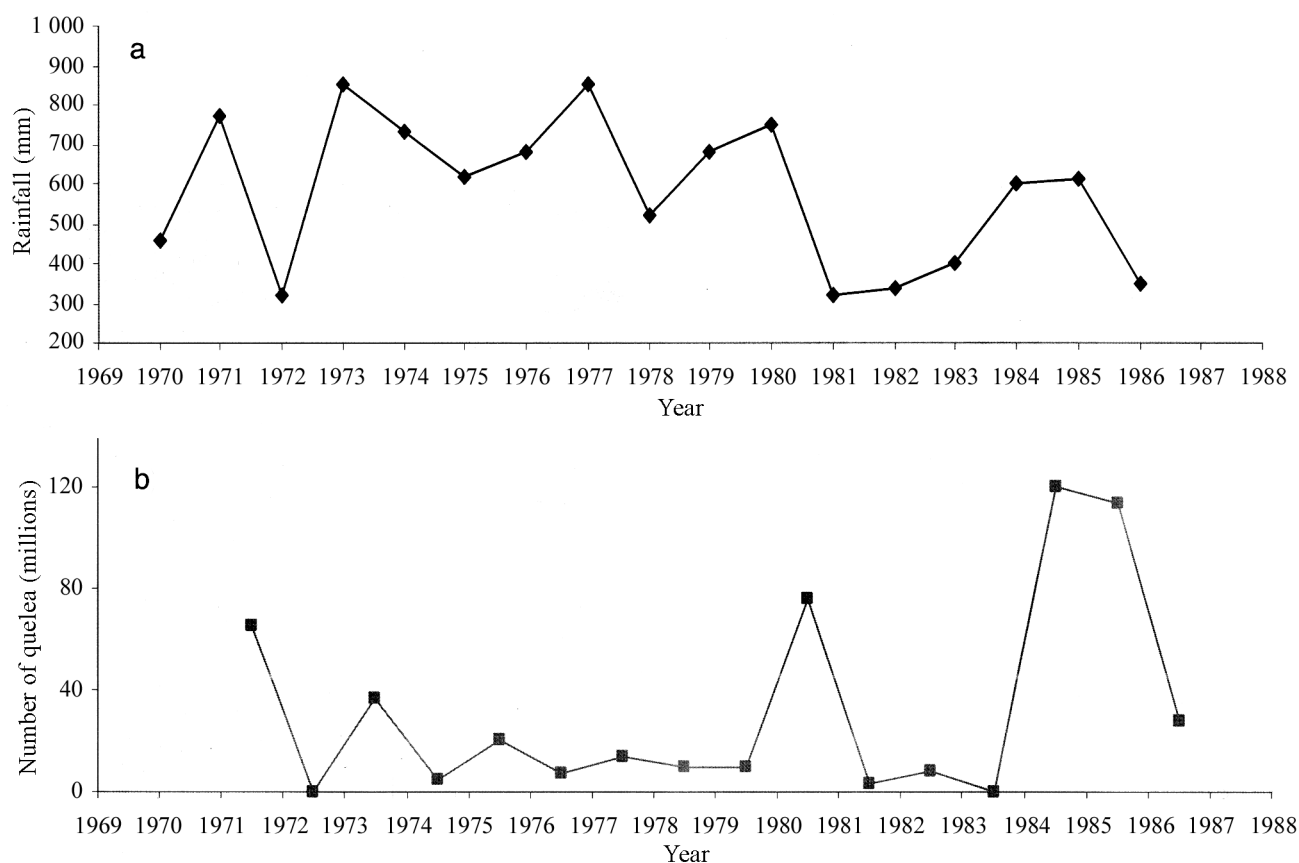


Fig. 1 Numbers of quelea controlled in Zimbabwe in winter compared with rainfall in the breeding areas in the previous summer. Data from La Grange (1989).

Mundy and Herremans (1997) estimated that between 65 and 180 million quelea are killed annually by control operations in the southern African region, but do not give details. If correct, it would mean that up to half the total post-breeding population is being exterminated annually, which seems unlikely given its wide distribution in the region and the low level of control in Namibia, Botswana and Mozambique. Nevertheless, a re-examination of the estimated population in southern Africa would clarify the situation.

4 Changes in quelea populations: numbers killed

La Grange (1989) presented data on the numbers of quelea controlled in Zimbabwe from 1972 to 1987 in relation to total rainfall in the main breeding areas (see Fig. 1). Kills fluctuated from 120 million to zero during this period, while the control effort was more or less constant. There is no evidence of a gradual increase over this 16 year period, even less of a population explosion. La Grange's claim of a loose correlation between rainfall in the breeding areas and subsequent population size is not supported by a re-plotting of the data and statistical analysis (Fig. 2). Zimbabwe contains a quelea population which is part of the southern Africa subspecies *Q.q.lathamii* (Jones, 1989a). Rainfall in Botswana, Mozambique and Angola would influence its breeding rate in those countries such that close correlation with rainfall should not be expected in Zimbabwe. An extensive winter wheat agriculture in Zimbabwe, the protection of which is the objective of most of the control operations, does not seem to have had any serious impact on quelea survival.

In South Africa control efforts have varied, partly for economic reasons and partly because of political changes. In the last ten years or so, "green lobby" pressure has led to use of environmentally-cleaner firebombs, rather than organophosphate pesticides; but the bombs are more expensive so that fewer targets can be tackled with the same level of funding. Political change is also putting more effort into protecting smallholder sorghum rather than wheat produced by commercial farmers. In the period 1956 to 1960, 400 million quelea were destroyed. Since then, the numbers have varied annually between 112 million in 1966/1967 (Crook

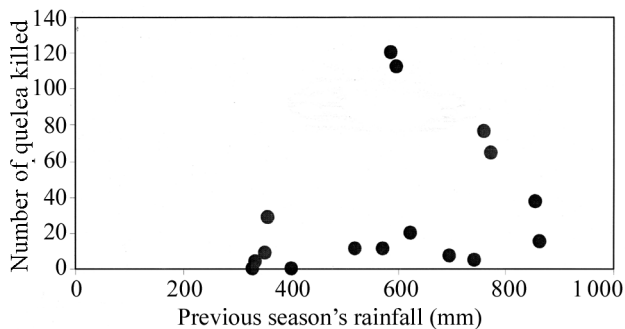


Fig. 2 Correlation of rain (mm) and number of quelea killed

$r = 0.300$, $P = 0.259$, n.s.; $Y = -4.37 + 6.31E-02X$, $R^2 = 9.0\%$

and Ward, 1968) and 39 million in 1999/2000. Although the data are incomplete, it appears that numbers fluctuate, and that while there is probably some correlation between numbers destroyed and the population level, there is no general upward trend in the population, as in Zimbabwe.

In Tanzania, reports on control effort were compiled by Magor (1970) for the period 1960 to 1969, and updated by P.J. Jones to 1976, as shown in Fig. 3. No information is provided as to how numbers were estimated, and they are probably exaggerated. Again there is evidence of large fluctuations, with no upward trend.

The final example comes from Nigeria where Ward and Jones (1977) estimated the numbers of birds destroyed over about 19 years, with a ten-year gap in the records (Fig. 4). The marked decline in the number of colonies found was ascribed to the drought afflicting the Sahelian region at that time, and not to control because similar declines were reported from nearby countries where there was no control. Once again, climatic factors, especially rainfall, were the main influence on quelea population size.

5 Changes in quelea populations: distribution

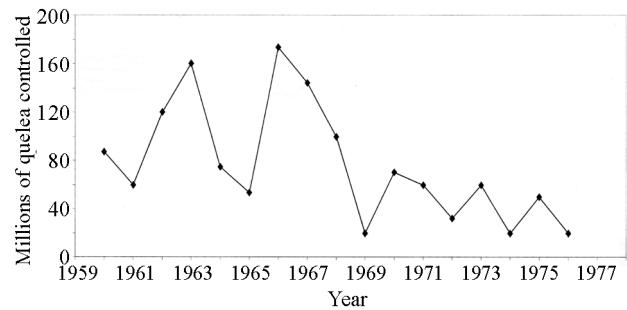


Fig. 3 The number of quelea controlled in Tanzania from 1960 to 1976

During the last four years, quelea were controlled only when threatening crops directly (data from Magor, 1970; updated by Jones, 1977).

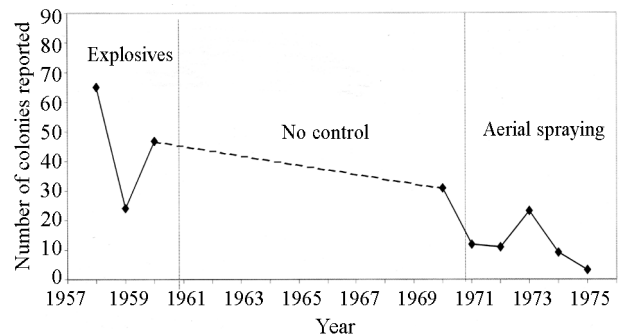


Fig. 4 The number of quelea breeding colonies found in Nigeria during two periods between 1958 and 1975 under different regimes of control

Those in 1958–1960 were found by ground survey and are underestimated. Those in 1970–1975 were found by ground/helicopter surveys, but, although more accurate, were sampled during drought (data from Ward and Jones, 1977).

It is possible that expanding and changing agro-eco-systems in Africa may be providing quelea with food during periods when it would otherwise be short, thereby encouraging overall growth in quelea populations.

The quelea was included in the South African Bird Atlas Project (SABAP) that sought, over a period of about ten years, to plot all observations of different bird species in quarter-degree squares in southern Africa. Although the quelea is not easy to identify out of breeding plumage, SABAP vetted records carefully and its published results should be reasonably reliable (Mundy and Herremans in Harrison et al., 1997). Whittington-Jones (1997) investigated the SABAP results in the light of historical accounts from 1910 to 1984, and concluded that the known distribution of the quelea had changed rapidly and dramatically from 1985 onwards. From an irregular visitor to the Eastern Cape, it had become widespread through most of that province. The coincidence of apparent expansion with the initiation of the SABAP in 1986 suggested that at least some of the expansion might have resulted from increased search effort. Even so, Whittington-Jones (1997) also investigated changes in agro-ecosystems as possible causes, as reviewed below.

In KwaZulu-Natal, in 1994–1995, Berruti (2000) reported quelea numbers in one area as 10 to 100 times higher than found by T.B. Oatley in 1970. However more information on rainfall in the two periods is needed to be sure that similar rain years are being compared. The only other recorded change (Ward and Jones, 1977) comes from the Lake

Chad Basin from the late 1950s to early 1970s, and also involves the whole Sahel. Large areas that had been used extensively for breeding in the 1950s in Nigeria bordering Lake Chad became desiccated by drought which began in 1965 and continued to 1972. The northern limit for breeding moved from just south of 15°N to just north of 13°N. The southern limit of the population appeared to remain the same, so the effect of the drought was to squeeze the quelea population into a narrower band of country. According to Ward and Jones (1977), the reduction in distribution was accompanied by a reduction in population size to 10% of the level it had been in 1960.

6 Changes in quelea populations: effects of agro-ecosystems

Over the past 100 years in Africa, agro-ecosystems have changed most in South Africa where organized commercial farming has long been established. Data on crop production are available by country on the agriculture statistics section of the FAO website (www.fao.org) for the period 1961 to 2001; and the areas under cultivation in South Africa are tabulated in Fig. 5. They show remarkably little shift over the last 40 years. Maize is the dominant cereal under about twice the hectareage of all other cereals together. The areas under wheat and sorghum have dropped in the last four years, too recently to have had an effect. Areas under millet and rice have apparently remained remarkably stable over the whole period, without any marked change in

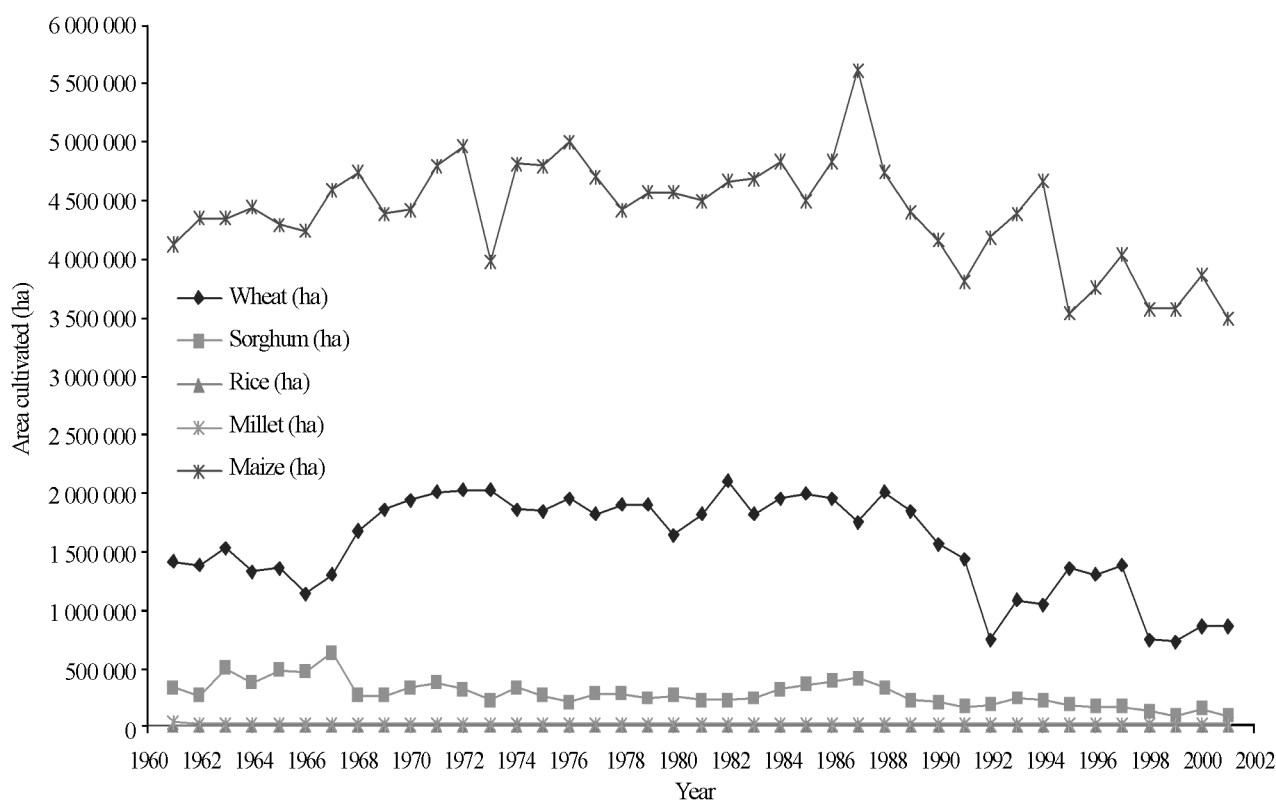


Fig. 5 Areas (ha) of cereal crops cultivated in South Africa from 1961 to 2001
Data from FAO website on agricultural statistics.

productivity or practices. From the quelea's point of view, inedible maize cultivation probably had a negative impact by replacing natural grasslands. Winter wheat or irrigated rice expansion, on the other hand, might have been positive.

Whittington-Jones (1997) noted that in the Eastern Cape, farming focused on livestock production up to the 1960s, then gradually changed to more intensive farming over the last three decades. Eight-fold and eleven-fold increases in wheat plantings were recorded in two districts, although the areas under cultivation are tiny in comparison with the province as a whole. He also addresses the possible influence of intensive livestock farming through supplementary feeding with crushed cereals including maize. Quelea have been seen consuming broken maize grain at cattle feedlots and at feeding trays put out for domesticated ostriches. In KwaZulu-Natal, sampled quelea show that crushed maize is the single most important food for the species outside the breeding season (Berruti, 1995). The question is whether these favorable micro-habitats have a significant bearing on the overall population.

Quelea have to drink at least twice, if not three times, a day. Flocks leaving roosts at first light often go first to water before going to feed. When it is hot, i.e. $> 40^{\circ}\text{C}$, flocks usually form day roosts near water in the heat of the day, during which they drink. They also drink in the evening on the way to roost. Whittington-Jones (1997) mentions the influence of the Orange-Great Fish River water transfer scheme that converted the Great Fish River from an intermittent to permanent water source. Allan et al. (1997) mention that in South Africa, 517 major reservoirs had been constructed by 1986 and that there are many tens of thou-

sands of earthen dams and boreholes on farms or other private land in southern Africa. These water sources allow quelea to exploit land that would not have been available before.

Whittington-Jones (1997) further mentions the possible influence of overgrazing through which woody species such as *Acacia karoo* have encroached into grasslands in the Eastern Cape. The acacia provides ideal nesting and roosting habitat and may have aided the spread of quelea into that province. In the same context, Crook and Ward (1968) cite the often repeated idea that overgrazing encourages annual grasses to flourish in place of perennials, to the advantage of quelea populations. While such an advantage may be occurring, it is not known if there is any published information that quantifies the extent to which this has happened.

Evidence from other countries is much less complete. Fig. 6 shows the changes in hectareage in principal cereal crops grown in a typical quelea country, Tanzania. Unlike circumstances in South Africa, some significant long-term changes are noticeable. Thus the staple and preferred food crop is maize and the 40 years from 1961 to 2001 have seen a quadrupling of the area under cultivation. In contrast, the number of hectares under sorghum has fluctuated after a steady increase from 200 000 to 550 000 ha by 1976. Rice cultivation has grown six-fold but wheat, after an initial surge to 60 000 ha in 1970, has also fluctuated.

Maize is unlikely to have had any positive influence in Tanzania, quelea only occasionally eating it as spillage when it has been pounded in villages. Rice is regularly eaten by quelea both before and after harvest, and control opera-

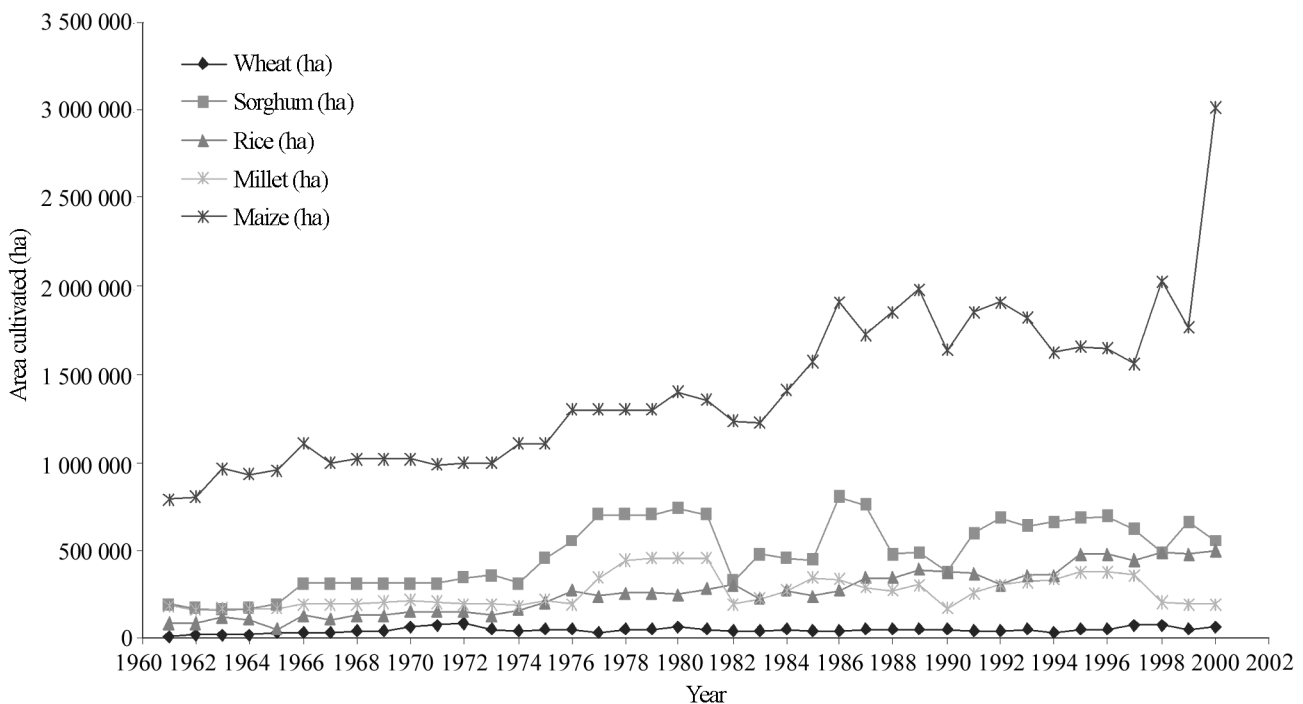


Fig. 6 Areas (ha) of cereal crops cultivated in Tanzania from 1961 to 2000
Data from FAO website on agricultural statistics.

tions try to reduce quelea numbers around major rice farms during vulnerable stages of the crop. However, flocks of quelea in the middle of Tanzanian irrigated rice farms often feed on wild grass seed (pers. obs.). Of 1 454 quelea sampled in a roost adjacent to rice farms in Cameroon, 64% were found to be feeding exclusively on rice and 22% exclusively on wild grass seed and insects (Elliott, 1979). Luder (1985) found that quelea in Tanzania caused more damage to wheat fields that had been badly weeded than those which were clean, indicating that quelea were attracted as much by associated weed seed.

Tanzania covers about 71 one-degree squares; quelea have been recorded in 47 of them, and a further 17 contain vegetation that is probably suitable for the species (Magor and Ward, 1972). Given this wide distribution, it must be questioned what effect a million hectares, roughly a single one-degree square, of small grain production grown during the rainy season when natural food is widely available, is likely to have on the quelea population. In contrast, human demographic pressure may be generating a negative impact that could balance out any benefit from changes in agro-ecosystems. For example, the human population in South Africa has increased from 12 million in 1951 to 39 million in 1991 (Reader, 1998). A parallel increase can be expected in Tanzania. In the latter, two effects are evident to the casual observer: the penetration of village communities deeper and deeper into the countryside, and the cutting of small trees for fuel. Most Tanzanian quelea establish breeding colonies well away from villages in patches of thorn trees. They need peace and quiet and trees to breed successfully.

7 Discussion

There is no shortage of statements that quelea populations are increasing and that the main reason for this is the extra food provided by agriculture (Lourens, 1963; Gaudchau, 1967; Mundy and Herremans, 1997; Brown and Tinney, 1998; Berruti, 2000). Some have also drawn attention to population reductions caused by drought, especially in the Sahel in the 1960s (Ward and Jones, 1977; GTZ, 1987). This paper has attempted to take a dispassionate view of the evidence, and to draw conclusions accordingly.

The first point to make is that it is not an easy task to assess population size in a bird as numerous as the quelea. Breeding colonies are conspicuous, and can be seen from the air several kilometers away. They are best searched for by helicopter, supported by information from local populations or farmers who have been encouraged to report colonies. Resources for such surveys and to maintain local networks are increasingly scarce, with the result that repeating surveys to standard is difficult. Indirect measurements of population sizes have been made from the kills achieved by control teams on the assumption that control effort is more or less constant. Where control effort changes, comparisons will be less valid.

All the evidence so far indicates that quelea populations fluctuate, influenced strongly by favorable rainfall for

breeding. During widespread drought, large declines can be expected. If drought is localized, emigration is likely to diminish any effect. If conditions are good over a large part of the range, breeding is not only likely to be successful but will often be repeated itinerantly in several different places as well (Jaeger et al., 1986).

Information from South Africa that suggests that the range for the quelea has expanded there (Whittington-Jones, 1997); but this is not necessarily evidence for a larger quelea population. It is possible that changes in agro-ecosystems, or simply human pressure, may be forcing the quelea to range further to survive. The numbers reaching the Eastern Cape are, by quelea standards, small; flocks seldom exceed a few hundred birds, and their contribution to overall numbers insignificant. Even the evidence given by Berruti (2000), that quelea are now 10–100 times more abundant in one part of KwaZulu-Natal than they were in the 1970s, is probably an indication of distributional change rather than exponential increase in overall population levels.

Changes in agro-ecosystems have been relatively minor with respect to cereal crops, even in South Africa, and have had little effect on quelea. Although quelea attack on small-grain crops is impressive, and causes much anguish to farmers and Governments, its impact compared to the vast tracts of savanna grassland that form the quelea's natural food source is still very small. On an even smaller scale are impacts on livestock feedlots and domestic ostrich feeding troughs that provide a ready source of food to a few quelea during the dry season. While such food sources might sustain small local populations of quelea, they are hardly likely to affect overall regional totals. Agro-ecosystems have probably had a positive effect on quelea in another area: the building of farm dams and larger scale reservoirs. As quelea can range about 30 km from a daily water supply, the presence of such dams should open substantial new areas for foraging. On the other hand, the presence of water without wild grass seed would have little benefit.

Demographic changes involving increasing human population and its exploitation of trees for fuel and the countryside for agriculture are probably acting as a counter-pressure to any tendency for agro-ecosystems to increase quelea populations. It is possible that if human population continues to increase in Africa as it has over the last 40 years, and HIV/AIDS does not reverse the trend, it is likely that suitable breeding habitats may gradually disappear. Unless it can become more tolerant of humans, the quelea could, in the long run, follow the fate of another highly gregarious, colonially-nesting species, the passenger pigeon (*Ectopistes migratorius*).

Thus it appears that, while quelea populations fluctuate primarily according to rainfall in their breeding areas, there is no evidence of a modern population explosion and little evidence even to support any general trend towards increased regional population levels.

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References

- Allan DG, Harrison JA, Herremans M, Navarro RA, Underhill LG, 1997. Southern African geography: its relevance to birds. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ ed. The Atlas of Southern African Birds, Vol. 1: Non-passerines. Johannesburg: BirdLife South Africa.
- Berruti A, 1995. An investigation into the biology of the red-billed quelea *Quelea quelea* in the Bergville-Winterton area of KwaZulu-Natal. Durban: Durban Nat. Hist. Mus., unpubl. report.
- Berruti A, 2000. The pest status and biology of the red-billed quelea in the Bergville-Winterton area. In: Cheke RA, Rosenberg J, Kieser M ed. Workshop on Research Priorities for Migrant Pests of Agriculture in Southern Africa, Plant Protection Research Institute, Pretoria, 24–26 March 1999. Chatham, UK: Natural Resources Institute.
- Brooke C, 1967. The heritage of famine in central Tanzania. Tanzania Notes and Records 67: 15–22.
- Brown CR, Tinney GM, 1998. Thermal relations of red-billed quelea: implications for extending distribution. Ostrich 69: 379.
- Crook JH, Ward P, 1968. The quelea problem in Africa. In: Murton RK, Wright EN ed. The Problem of Birds as Pests. London: Academic Press.
- Elliott CCH, 1979. The harvest time method as a means of avoiding quelea damage to irrigated rice in Chad/Cameroun. J. Appl. Ecol. 16: 23–35.
- Elliott CCH, 1989. The pest status of the quelea. In: Bruggers RL, Elliott CCH ed. *Quelea quelea*: Africa's Bird Pest. Oxford: Oxford University Press.
- Elliott CCH, 1990. The migrations of the red-billed quelea *Quelea quelea* and their relation to crop damage. Ibis 132: 232–237.
- Erickson WA, 1989. Feeding ecology of quelea. In: Bruggers RL, Elliott CCH ed. *Quelea quelea*: Africa's Bird Pest. Oxford: Oxford University Press.
- Gaston A, 1976. Travaux phyto-écologiques en relation avec la lutte contre *Quelea quelea*. Rapport Final, Phase I et II. Projet régional no: RAF/67/587. Rome: FAO.
- Gaudchau MD, 1967. Report on control of the red-billed weaverbird (*Quelea quelea aethiopica*) in the Republic of the Sudan during 1964/65/66/67. Khartoum, Sudan: Ministry of Agriculture, Plant Protection Division, unpubl. report.
- GTZ (Deutsche Gesellschaft für Technische Zusammenarbeit), 1987. The Ecology and Control of the Red-billed Weaver Bird (*Quelea quelea* L.) in Northeast Nigeria. Eschborn, Germany: GTZ.
- Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ, 1997. The Atlas of Southern African Birds, Vol. 1: Non-passerines. Johannesburg: BirdLife South Africa.
- Jaeger MM, Erickson WA, 1980. Levels of bird damage to sorghum in the Awash Basin of Ethiopia and the effects of the control of quelea nesting colonies (1976–1979). Proceedings of the 9th Vertebrate Pest Conference, 9. Fresno, California: 21–28.
- Jaeger MM, Bruggers RL, Johns BE, Erickson WA, 1986. Evidence of itinerant breeding of the red-billed quelea *Quelea quelea* in the Ethiopian Rift Valley. Ibis 128: 469–482.
- Johnston, 1907. Destructive birds. J. S. Afr. Orn. Union 3: 135–136.
- Jones PJ, 1989a. Distribution, populations, and migration patterns of quelea in southern Africa. In: Bruggers RL, Elliott CCH ed. *Quelea quelea*: Africa's Bird Pest. Oxford: Oxford University Press.
- Jones PJ, 1989b. Quelea population dynamics. In: Bruggers RL, Elliott CCH ed. *Quelea quelea*: Africa's Bird Pest. Oxford: Oxford University Press.
- La Grange M, 1989. The effects of rainfall on the numbers of queleas destroyed in Zimbabwe. In: Mundy PJ, Jarvis MJF ed. Africa's Feathered Locust. Harare: Baobab Books.
- Layard EL, 1867. The Birds of South Africa. Cape Town: J.C. Juta.
- Lourens DC, 1963. The Red-billed Quelea. A Contribution to the Bio-ecology and Control. D.Sc. thesis. Pretoria: Faculty of Agriculture, University of Pretoria.
- Luder R, 1985. Weeds influence red-billed quelea damage to ripening wheat in Tanzania. J. Wildl. Manag. 49: 646–647.
- Magor JI, 1970. Control operations against *Quelea quelea* in Tanzania during the period 1960–1969, updated by P.J. Jones to 1976. London: Centre of Overseas Pest Research, unpubl. report.
- Magor JI, Ward P, 1972. Illustrated descriptions, distribution maps, and bibliography of the species of quelea (Weaverbirds: Ploceidae). Trop. Pest Bull. 1: 1–23.
- Miracle MP, 1965. The introduction and spread of maize in Africa. J. Afr. Hist. 6: 39–55.
- Mundy PJ, Herremans M, 1997. Red-billed quelea *Quelea quelea*. In: Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ ed. The Atlas of Southern African Birds, Vol. 1: Non-passerines. Johannesburg: BirdLife South Africa.
- Reader J, 1998. Africa: A Biography of the Continent. England: Penguin Books.
- Schlupp WF, 1922. The granivorous bird problem. J. Dept. Agric. Un. S. Afr. 4: 432–446.
- Ward P, 1965. The feeding ecology of the black-faced dioch *Quelea quelea* in Nigeria. Ibis 107: 173–214.
- Ward P, 1971. The migration patterns of *Quelea quelea* in Africa. Ibis 113: 275–297.
- Ward P, Jones PJ, 1977. Quelea Investigations Project, Nigeria: Final Report 1972–1975. London: Centre for Overseas Pest Research.
- Whittington-Jones CA, 1997. Apparent range expansion of the red-billed quelea *Quelea quelea* in the Eastern Cape Province of South Africa. Ostrich 68: 97–103.
- Wilson CE, 1947. The Sudan dioch in grain growing areas. Sudan Notes and Records 28: 151–156.