

# Are there two subspecies of Red-billed Quelea, *Quelea quelea*, in southern Africa?

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Two subspecies of the Red-billed Quelea, *Quelea quelea lathamii* and *Q. q. spoliator*, have been described from southern Africa on the basis of differences in dorsal colouration in non-breeding plumage, but the validity of *spoliator* has often been challenged. We examined museum specimens of both subspecies, including paratypes of *spoliator*, and recorded plumage characters of breeding and non-breeding queleas in the wild. These data suggest that 'typical' *lathamii* and *spoliator* merely represent two extremes of a continuous variation in colour, with the majority being intermediate. Significantly, breeding males whose plumage types span the range between *spoliator* and *lathamii* occur together in the same colonies. Furthermore, variation in male nuptial colouration, which has provided the basis for distinguishing the subspecies of Red-billed Queleas elsewhere in Africa, shows no association with differences in dorsal plumage colour. We also present data on the timing of breeding of the two taxa which suggest that reproductive isolation sufficient to maintain two separate subspecies within southern Africa is unlikely to occur. We conclude, therefore, that because *spoliator* individuals cannot be reliably separated from *lathamii* on morphological criteria and, because both forms are likely to breed in the same places at the same times, the subspecies *spoliator* does not reflect any meaningful phylogenetic division. The Red-billed Quelea is therefore represented by *Q. q. lathamii* alone in southern Africa.

## INTRODUCTION

The Red-billed Quelea, *Quelea quelea*, was originally thought to be represented by only one subspecies in southern Africa, *Q. q. lathamii*. However, a second subspecies *spoliator* was later described from KwaZulu-Natal (Clancey 1960), and claimed to be typical of birds breeding in the more mesic areas of the central highveld and northeast coast of South Africa, Swaziland and southern Mozambique, i.e. the southeastern part of the formerly-accepted range of *lathamii* (Fig. 1). Subsequent work by Clancey (1968, 1973), based on museum specimens identified by him as *spoliator*, suggested that this subspecies also occurs during the non-breeding season (May to November) throughout the interior of southern Africa within the breeding range of *lathamii*.

The subspecific status of *spoliator* has remained controversial. It was described from specimens in non-breeding plumage that had 'colder' grey-brown upperparts compared to the warm buff-brown of 'true' *lathamii*. The new race was rejected by Lourens (1961) and Ward (1966) as being simply one colour variant of a highly variable population and not reliably distinguishable from *lathamii*. In particular, Lourens (1961) claimed that the two forms bred together and that the offspring of either form could be light- or dark-backed, though he presented no data in support. The new subspecies was accepted by Irwin (1981) for Zimbabwe but was not mentioned in the standard works for Malawi and Zambia (Benson & Benson 1977; Benson

*et al.* 1973). A recent review of range expansion by Red-billed Queleas in the Eastern Cape of South Africa, at the southern limit of their distribution where they might be expected to be *spoliator*, did not refer these birds to particular subspecies and pointed out that better diagnostic characteristics were required (Whittington-Jones 1998).

The validity of *spoliator* is particularly difficult to assess, because all other subspecies of the Red-billed Quelea had been characterized by the type and frequencies of the different plumage morphs of males in breeding dress (Ward 1966). Male Red-billed Queleas retain the same colour-morph when they moult into their breeding plumage each year, and it is known that the colour morphs are strongly heritable (Dale 2000). Morph frequencies are reliably quantified only in large, randomly-sampled collections of breeding males (Ward 1966, 1973), which has still not been done for *spoliator*. The small data set on male breeding plumage colouration given by Clancey (1973) is inadequate for the purpose (see below), while the extent of variation in dorsal colouration has not been described for any other subspecies, including *lathamii*.

Apart from the equivocal morphological evidence, ecological and behavioural considerations also argue against the validity of *spoliator*. Throughout Africa, Red-billed Queleas are obliged to perform regular seasonal migrations in response to the rainfall patterns that determine the availability of their grass seed food. Regional differences in the timing and direction of migration limit contact between adjacent populations, and the resulting genetic isolation is reflected in the geographical separation of different subspecies (Ward 1971; Jones 1989a). In southern

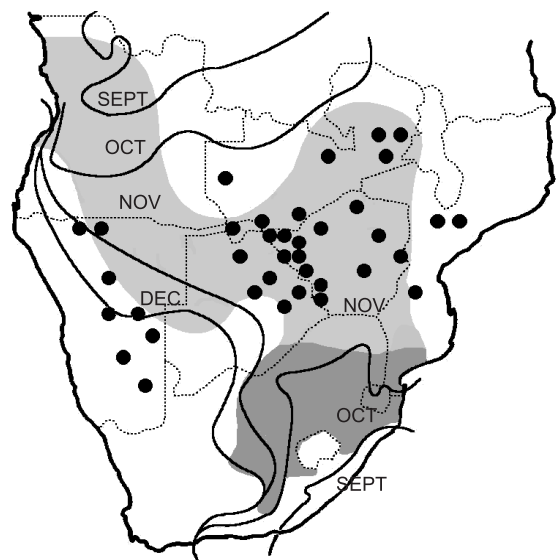


FIG. 1. Supposed breeding ranges of *Quelea q. lathamii* (light grey) and *Q. q. spoliator* (dark grey) in southern Africa (adapted from Magor & Ward 1972 and Clancey 1973). Black dots indicate records of *spoliator* during the non-breeding season (May to November) within the range of *lathamii* (Clancey 1973). Contours indicate the approximate start of the wet season (Thompson 1965).

Africa, however, this is not the case, because both *lathamii* and *spoliator* would be expected to respond in similar ways to the timing and distribution of rainfall, such that they would remain sympatric for much of the year (Jones 1989b). The suggested breeding range of *spoliator* roughly corresponds with the region of southern Africa that receives its first rain in October (Fig. 1). Large numbers of queleas remain there throughout the dry season, but must emigrate as their grass seed food germinates when the rains begin. The only suitable habitat available to them at this time lies to the north and west in what Clancey (1973) delimited as the breeding range of *lathamii*, where it has not yet rained. By late November, however, it has begun raining throughout the *lathamii* range as well and all birds, both immigrant *spoliator* and indigenous *lathamii*, must perform an 'early-rains migration' to regions of earlier rainfall where fresh seed has by now matured. Large numbers of queleas, presumably both *lathamii* and *spoliator*, fly southeastwards to early-rains quarters that correspond with the breeding range of *spoliator*, where they begin breeding (Ward 1971; Jones 1989b).

Despite this sequence of events, which seems to ensure that *lathamii* and *spoliator* will breed sympatrically, it is conceivable that some genetic isolation could occur if *spoliator* responds to the region's earlier rainfall by beginning pre-nuptial moult and gonad development sooner than *lathamii*, which do not experience the first rainfall until 1–2 months later. Thus, by the time *spoliator* have been pushed ahead of the rains into the *lathamii* range, and then made the ensuing return early-rains migration in company with *lathamii*, they are already ready to breed. Because events in the breeding cycle are so highly synchronized within a colony (Ward 1965, 1971), birds that are out of phase with the majority normally breed elsewhere. In this case, later-maturing *lathamii* individuals will have returned part-way along the track of their 'breeding migration' and out of the *spoliator* breeding range before they are ready to establish their first colonies. Such a possibility has not previously been investigated.

In this paper we re-assess the plumage characteristics used to separate *lathamii* and *spoliator*. We re-examine museum specimens of the two taxa and we present new data on dorsal plumage colour and the frequencies of colour morphs of males in breeding plumage collected across the breeding ranges of *lathamii* and *spoliator* in South Africa, Botswana and Zimbabwe. We also investigate whether there might be differences in the timing of breeding of *lathamii* and *spoliator* sufficient to maintain some degree of genetic isolation between them by comparing their timing of pre-nuptial moult and testis development.

## MATERIALS AND METHODS

### Museum specimens

R.A.C. and M.D. independently examined 28 specimens of *lathamii* and 50 specimens of *spoliator*, including nine paratypes of *spoliator*, lent to us by the Durban Natural Science Museum (Appendix IA); all were in non-breeding plumage. Based on the criteria given by Clancey (1960), they assigned each specimen to a category according to the colour of the dorsal contour plumage on a scale from 1 (typical *spoliator*) to 4 (typical *lathamii*) with categories 2 and 3 intermediate. Category 1 denoted dorsal feathers whose pale whitish edges contrasted strongly with their dark brown centres, giving an overall 'cold' appearance, and 4 denoted lighter brown dorsal feathers whose edges were a much less contrasting buff-brown, giving a 'warm' appearance.

P.J.J. and R.A.C. examined all the specimens of Red-billed Queleas held by the Natural History Museum of Zimbabwe, Bulawayo, that had been identified and labelled by P.A. Clancey (M.P.S. Irwin, pers. comm.) as either *lathamii* (23 specimens) or *spoliator* (18 specimens); all were in non-breeding plumage. Each

specimen was assigned by consensus between P.J.J. and R.A.C. to one of the plumage categories described above (Appendix IB).

### Plumage colouration among breeding birds

The standard methods for quantifying morph frequencies are based on Ward (1966, 1973), who recorded i) the extent to which the black facial mask extends as a frontal band above the bill; ii) the proportion of males in which the facial mask is white, not black; iii) the shade of yellow colouration (light to dark golden-yellow) on the crown and breast; and iv) the percentage of birds in which the yellow colouration is variably suffused with light pink to dark red. Measures (i) and (ii) have together become known as the 'mask index' among quelea workers and have been routinely recorded in several countries to 'fingerprint' populations in order to trace their movements (e.g. Jaeger *et al.* 1989).

Extensive data on male polymorphism frequencies exist from 19 collections ( $n = 119$ –1247) made in South Africa during the 1950s and 60s (Lourens 1957, 1960, 1963). The collecting localities for these samples were not stated but D.C. Lourens (pers. comm.) identified those given in his thesis (Lourens 1963). A further eight collections ( $n = 96$ –649) were made by P.J.J. in northwestern Botswana in the early 1970s.

All birds in each sample were scored for whether the facial mask was white or black, and for the presence or absence of any pink colouration on the crown and breast. In none of these samples was there any significant association ( $\chi^2$ -values all n.s.) between mask colour (white or black) and the colour of the crown and breast (pink or buff). These two characters therefore appear to be expressed independently of each other (Dale 2000), and are treated as such in the following analyses.

In 1998 a much more detailed data set was collected by M.D. for males at four breeding colonies in Zimbabwe, within the supposed breeding range of *lathamii*. Two were in the Save River catchment in southeastern Zimbabwe (Malilangwe 21° 05'S, 31° 55'E,  $n = 105$ ; Senuko 20° 45'S, 31° 50'E,  $n = 88$ ) and two in the Zambezi valley (Bumi Hills 16° 54'S, 28° 12'E,  $n = 99$  and Maitengwe 19° 55'S, 27° 05'E,  $n = 96$ ). In addition to being scored for the colour of their dorsal plumage as before, males were also scored for various measures of their breeding plumage, including 'mask index' (Ward 1966), width of forehead band (in mm) and depth of frontal 'bib' (mm), crown colour (1–4, buff to pink), intensity of crown colour if buff (1–3, light to dark), breast colour (as crown colour), intensity of breast buff colour (as for crown), extent of grey scaly feathers on belly (1–4, no grey to all grey; this feature is distinctive of *lathamii*, as opposed to races in East and West Africa), the underlying colour of belly feathers (0 none, 1 buff, 2 mixed, 3 pink), and belly colour intensity (0–3, no colour to dark). All scores were assigned by M.D. alone.

### Plumage variation in non-breeding birds and the timing of pre-nuptial moult and testis growth

If *spoliator* comes into breeding condition sooner than *lathamii*, this should be expressed as an earlier onset of the pre-nuptial moult amongst males. It should be most obvious among the mixed population of immigrant *spoliator* and indigenous *lathamii* present within the dry season range of *lathamii* as the rains begin in November. A night roost containing birds beginning the pre-nuptial moult was sampled in Bulawayo, Zimbabwe, on 22 and 23 November 1997 as the birds were undergoing pre-migratory fattening prior to the 'early-rains migration' out of the region. All birds were classified from 1 to 4 (typical *spoliator*, intermediate, or typical *lathamii*), in the same manner as described above for the museum specimens. All were sexed by dissection. Males were further classified according to the progress of the pre-nuptial moult on a scale from 0 (not yet

started) to 6 (full breeding plumage) and their testes were measured (longest axis to the nearest 1 mm). The females' ovaries were all inactive.

## RESULTS

### Museum specimens

We anticipated that plumage abrasion and exposure to sunlight might contribute to a faded, 'colder' appearance. Some museum specimens were clearly more worn and faded than others, depending on whether they were collected before or after the post-nuptial moult (May–September in southern Africa), yet worn birds showed the same range of dorsal colouration as fresh ones. Among a large sample of birds in the Natural History Museum of Zimbabwe we could find no correlation between plumage score and collecting date. Moreover, Clancey's type specimen of *spoliator* was collected in November in quite fresh plumage, and before the breeding season when the most rapid wear and fading occur. For these reasons, and because we were investigating the attributions made by others on the specimens available, we did not take account of plumage wear in our comparisons of museum specimens collected at different times of year.

There was wide variation in dorsal plumage colouration among specimens of both *lathamii* and *spoliator* obtained from the Durban Natural Science Museum (Fig. 2). Although R.A.C. and M.D. did not completely agree, there was exact concurrence between their rankings for 50% of the specimens (39 of 78), and the disparity (33 of the remainder by one score category only, six by two categories) reflects the subjectivity involved. There was close agreement, however, on the scoring of the nine paratypes examined of *spoliator*, two of which (nos 10892 and 10898) were agreed to be indistinguishable (score 3) from specimens classified by the Durban Museum as representative of *lathamii*. Most specimens appeared to be intermediate between the states described by Clancey (1960) as typical of *lathamii* and *spoliator*.

P.J.J. and R.A.C. were similarly astonished by the large proportion of the specimens in the Natural History Museum of Zimbabwe labelled as either *lathamii* or *spoliator* by P.A. Clancey that appeared intermediate between the two 'typical' states (Fig. 3). Indeed, the 41 specimens could be arranged in an unbroken continuum from warm brown to cold grey, within which an independent third observer (P.J.M.) was unable to identify correctly any disjunction between the two taxa.

### Re-examination of the plumage data for *lathamii* and *spoliator*

#### Dorsal plumage colouration among non-breeding birds

In the sample of non-breeding birds collected from Bulawayo in 1997, there was no difference in the frequencies of dorsal plumage categories between males and females ( $n = 155$  and  $76$ , respectively,  $\chi^2_3 = 1.54$ ,  $P = 0.67$ ), so these were combined. 'Typical' *spoliator* and *lathamii* birds made up only a small proportion of the sample. There was a continuous range of colour variation in mantle plumage from 'cold grey' to 'warm buff' and most scores were intermediate, either 2 or 3 (Fig. 4a). There is no evidence, therefore, that two distinct subspecies can be readily identified among non-breeding birds.

#### Morph frequencies of male *spoliator* and *lathamii* in breeding plumage

Clancey (1973) presented some limited information on the relative frequencies of white- and black-faced morphs and the extent of pink colouration among *lathamii* and *spoliator* males, but he did not make any explicit claim that differences could be found between them. Statistical analysis of his data set (Table 1)

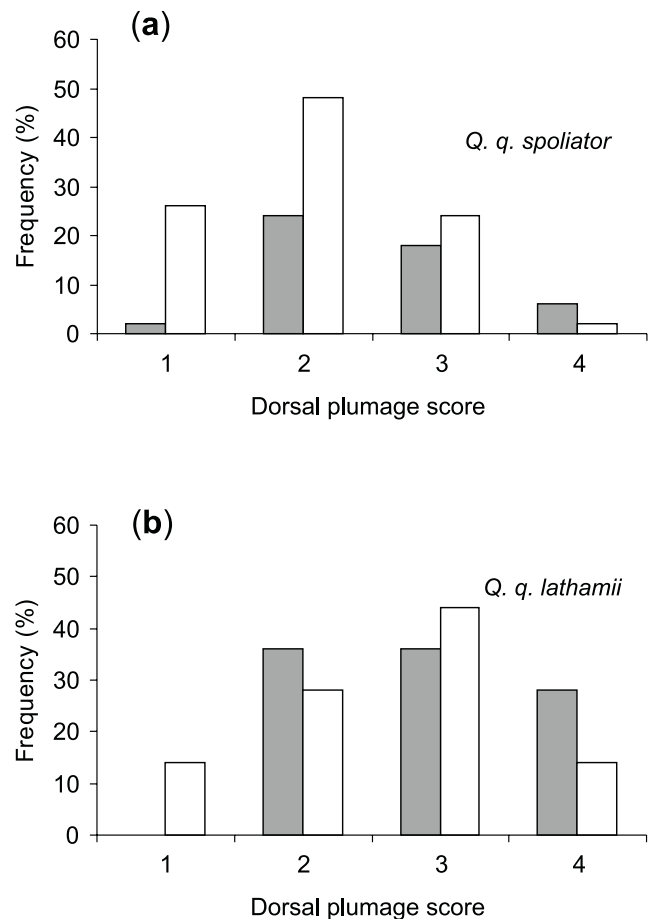


FIG. 2. Dorsal plumage scores assigned independently by R.A.C. (open bars) and M.D. (grey bars) to specimens of Red-billed Queleas in the Durban Natural Science Museum labelled as: (a) *Quelea q. spoliator* ( $n = 50$ ) and (b) *Q. q. lathamii* ( $n = 28$ ). Scores are (1) typical *spoliator*, (2) and (3) intermediate, (4) typical *lathamii*. Sexes are combined on the basis that no sexual differences could be found in plumage colour in fresh specimens (see text).

shows that there is no significant difference in the frequencies of white-faced males between *lathamii* and *spoliator* ( $\chi^2_1 = 0.032$ ,  $P = 0.86$ ) nor in the proportions showing pink colouration ( $\chi^2_1 = 0.731$ ,  $P = 0.39$ ). Because of the small sample sizes involved, especially of *spoliator*, perhaps no great reliance should be placed on this result.

More meaningful comparisons can be made, however, among much larger data sets from South Africa, Zimbabwe and Botswana that have remained unanalysed since the data were

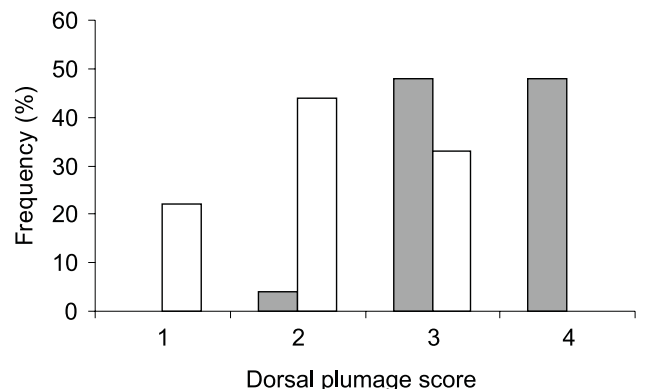


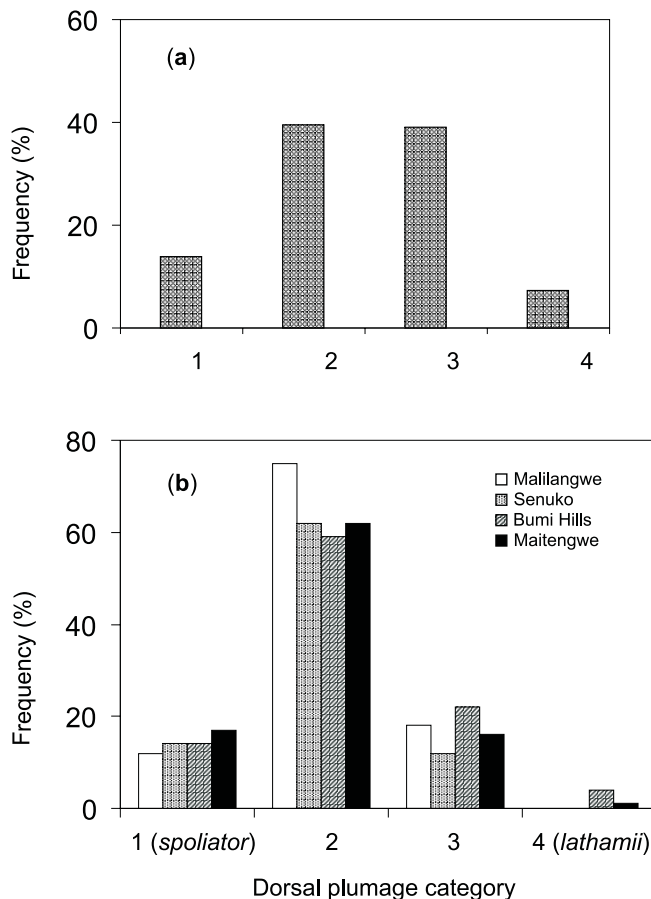
FIG. 3. Dorsal plumage scores assigned by consensus between R.A.C. and P.J.J. to specimens of Red-billed Queleas *Quelea q. lathamii* ( $n = 23$ , open bars) and *Q. q. spoliator* ( $n = 18$ , grey bars) in the Natural History Museum of Zimbabwe. Scores as in Fig. 1. Sexes are combined on the basis that no sexual differences could be found in plumage colour in fresh specimens (see text).

**TABLE 1. Relative frequencies of colour morphs of breeding male *Quelea q. lathamii* and *Q. q. spoliator* (from Clancey 1973). Males were classified according to whether the facial mask was black or white, and whether the buff of the head and neck was suffused with pink.**

	<i>lathamii</i>	<i>spoliator</i>	Total
White mask; buff	5	1	6
White mask; pink	14	3	17
Black mask; buff	29	9	38
Black mask; pink	52	10	62
Totals	100	23	123

collected some decades ago (Lourens 1957, 1960, 1963, P.J.J. unpubl.). Some of these samples came from within the suggested breeding range of *spoliator*, according to Clancey's (1973) map, and can be compared with the remainder, which were from within the breeding range of *lathamii* (Table 2). The combined data sets comprising only supposed *lathamii* individuals showed no significant heterogeneity in the percentage of white-faced males ( $\chi^2_{12} = 11.33$ ,  $P = 0.50$ , Table 2a). The mean was 13.6% white-faced, with the two extreme values (10% and 17%) both recorded in relatively small (c.100 birds) samples from Botswana. These frequencies closely matched those given for *lathamii* without localities in Lourens (1957), where the mean was 12.7% white-faced morph ( $n = 2525$ ) and the range was 10.7–16.0%.

By contrast, the six samples from within the *spoliator* breeding range showed significant heterogeneity ( $\chi^2_5 = 30.11$ ,  $P < 0.001$ , Table 2b). Four of these, however, showed no differences from the preceding *lathamii* samples (mean 13.1%, range 12.2–14.0%). The heterogeneity is entirely attributable to two quite large samples with unusually low frequencies of white-faced morphs (Settlers 5.4%, Bethlehem 5.1%), though other colonies at the same localities had normal white-morph frequencies (Settlers

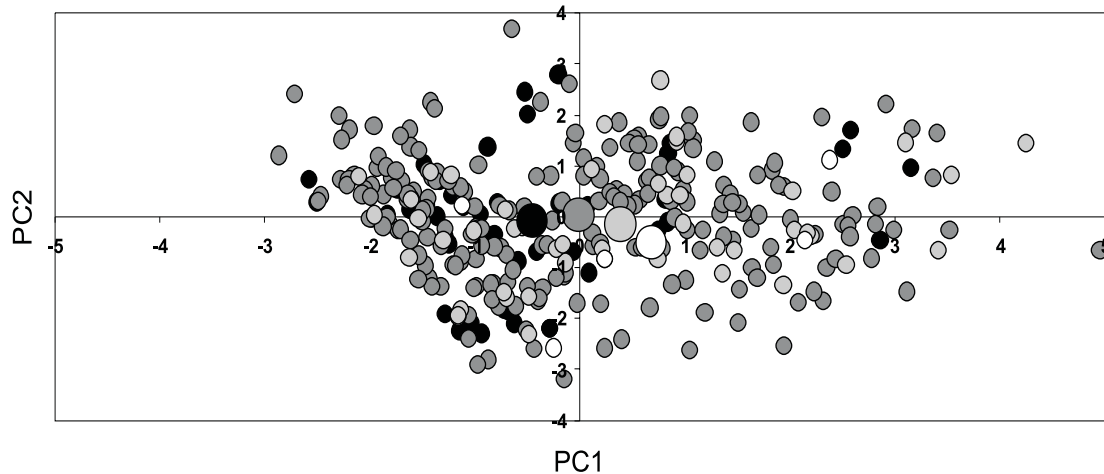


**FIG. 4. Frequency distributions of *spoliator*-type, *lathamii*-type, and intermediate Red-billed Queleas in Zimbabwe, based on dorsal plumage colouration. a, Early-rains birds in non-breeding plumage (no difference between males and females, sexes therefore combined,  $n = 230$ ); b, breeding males from four colonies ( $n = 105, 88, 99, 96$ , respectively).**

**TABLE 2. Frequencies of breeding male Red-billed Queleas with white facial mask and pink suffusion on the crown and breast from breeding colonies of (a) *Quelea q. lathamii* in Botswana, Zimbabwe and South Africa, and (b) *Q. q. spoliator* in South Africa.**

(a) <i>lathamii</i> localities	<i>n</i>	% White-faced	% Pink
Sheho's, Botswana <sup>(1)</sup> ; 20° 05'S, 23° 55'E	446	12.8	51.3
Komaneng, Botswana <sup>(1)</sup> ; 20° 10'S, 23° 15'E	649	13.4	48.4
Modisaemang's, Botswana <sup>(1)</sup> ; 20° 45'S, 23° 40'E	387	13.2	59.2
Maun, Botswana <sup>(1)</sup> ; 20° 05'S, 23° 30'E	258	15.5	47.3
Kudumane, Botswana <sup>(1)</sup> ; 18° 55'S, 23° 55'E	400	16.0	51.6
Lake Ngami, Botswana <sup>(1)</sup> ; 20° 25'S, 22° 50'E	239	11.7	56.1
Serowe, Botswana <sup>(1)</sup> ; 22° 35'S, 26° 45'E	102	9.8	56.7
Toteng, Botswana <sup>(1)</sup> ; 20° 15'S, 22° 50'E	96	16.7	37.5
Mahalapye, Botswana <sup>(2)</sup> ; 23° 05'S, 26° 50'E	317	12.0	53.0
Sabi River, Zimbabwe <sup>(2)</sup> ; 21°S, 32°E	348	13.8	51.1
Limpopo River, South Africa <sup>(2)</sup> ; 23°S, 28°E	384	10.7	46.9
Limpopo River <sup>(2)</sup>	481	13.3	50.1
Limpopo River <sup>(2)</sup>	950	15.2	48.6
Total/mean	5057	13.6	50.6
(b) <i>spoliator</i> localities	<i>n</i>	% White morph	% Pink
Settlers, South Africa <sup>(2)</sup> ; 25° 00'S, 28° 30'E	371	5.4	51.5
Settlers <sup>(2)</sup>	1247	12.8	50.9
Settlers <sup>(2)</sup>	763	14.0	56.6
Bethlehem, South Africa <sup>(2)</sup> ; 28° 15'S, 28° 20'E	216	5.1	59.2
Bethlehem <sup>(2)</sup>	931	13.1	53.4
Pretoria, South Africa <sup>(2)</sup> ; 25° 45'S, 28° 12'E	262	12.2	54.2
Total/mean	3790	11.9	54.9

<sup>(1)</sup>P.J.J. (unpubl.); <sup>(2)</sup>Lourens (1963).



**FIG. 5.** A principal component scatterplot of plumage variation among breeding male Red-billed Queleas categorized as 1 = *spoliator*-type (black circles); 2, 3 intermediate (dark and light grey circles); 4 = *lathamii*-type (open circles) on the basis of their dorsal plumage colouration. Large symbols indicate means of each distribution. 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 belly. A higher PC2 score indicates a greater width of the black facial mask above and below the beak. There are no discrete clusters of individuals associated with the prior classification into *spoliator*- or *lathamii*-type and the category means are closely grouped in the centre of the distribution.

12.8%, Bethlehem 13.1%). Assuming that the samples were unbiased, the biological significance of these differences and whether they have any relevance to the problem of typifying *spoliator*, is unknown.

The variation in the frequencies of males with a pink suffusion to the breeding plumage shows an altogether different pattern. Birds collected within the *spoliator* breeding range show 54.9% with pink crown and breast (range 50.9–59.2%,  $n = 3690$ ; Lourens 1963), with no significant heterogeneity among samples ( $\chi^2_5 = 10.01$ ,  $P = 0.075$ ). By contrast, there is significant heterogeneity among samples from the *lathamii* breeding range ( $\chi^2_{12} = 29.5$ ,  $P = 0.003$ ). Although the frequencies of pink colouration in many colonies are similar to the values for *spoliator*, the overall mean value is 50.6% (range 37.5–59.2%,  $n = 5057$ ; Lourens 1963, P.J.J. unpubl.) and the source of the heterogeneity appears to be Modisaemang's colony in Botswana with the highest percentage of pink males. If this sample is removed from the analysis, no statistically significant heterogeneity remains ( $\chi^2_{11} = 17.06$ ,  $P = 0.106$ ); the removal of no other sample has this effect. As before, the biological significance of this is unknown.

Our more recent and much more detailed data sets from breeding colonies in Zimbabwe show two things. First, it is clear that both *spoliator*-like and *lathamii*-like individuals occur together in the same colonies (Fig. 4b), thereby offering some support to the earlier claim by Lourens (1961) that the two forms breed together. There were no significant differences in dorsal plumage scores among the four colonies ( $\chi^2_9 = 13.2$ ,  $P = 0.15$ ), though it is curious that extreme *lathamii*-like birds (dorsal score 4) were scarce and indeed apparently absent from southeastern Zimbabwe, despite having been present in Bulawayo at the start

of the rains (Fig. 4a).

Second, we found no significant association between male breeding plumage colouration and *spoliator*-like or *lathamii*-like dorsal plumage. In a principal components analysis of the detailed measures of male breeding colouration in relation to their dorsal plumage scores, a positive PC1 indicated a pinker, more deeply-coloured belly and a lesser extent of grey, scaly feathers on the belly. A higher PC2 score indicated a greater extent of the black facial mask above and below the beak. PC1+PC2 accounted for more than 50% of the variation in male plumage pattern, yet no discrete clusters of individuals could be identified with respect to dorsal plumage score and the category means are all closely grouped in the centre of the distribution (Fig. 5).

#### Timing of the pre-nuptial moult of *lathamii* and *spoliator*

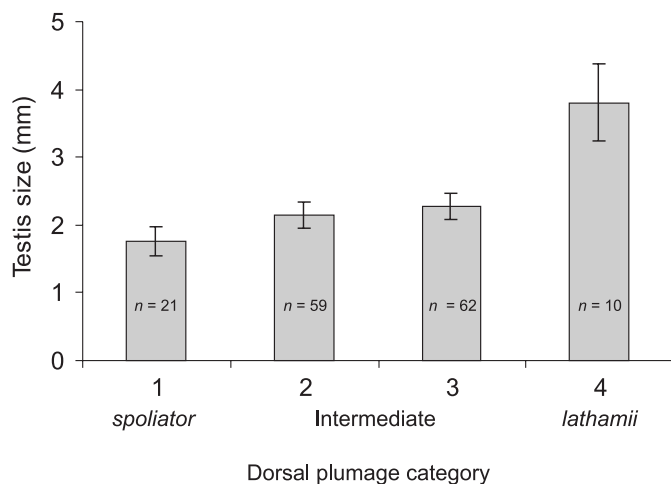
The results from the night roost of pre-migratory birds sampled in Bulawayo were unexpected. Although there were indeed significant differences in the progress of both their pre-nuptial moult (Table 3) and testis growth (Fig. 6) among males having different dorsal plumage scores, *lathamii* males were further advanced in readiness to breed than the *spoliator* individuals. Whatever the reason for this, and we have no explanation for it, it is the opposite of the suggestion that *spoliator* might come into breeding condition sooner than *lathamii*.

#### DISCUSSION

The available data suggest that the cold-grey '*spoliator*'-like and warm-buff '*lathamii*'-like colouration of the dorsal plumage of Red-billed Queleas in non-breeding dress merely represent

**TABLE 3.** Numbers of male Red-billed Queleas at each stage of their pre-nuptial moult, classified according to the colour of the dorsal plumage (Clancey 1960): 1 = pale whitish edges to the mantle feathers giving a 'cold-grey' appearance, closely resembling *spoliator*; 4 = warm buff edges to the mantle feathers, typical of *lathamii*. Pre-nuptial moult scores are: 0 = not yet started; 1 = just started; 2+3 = 1/4–1/2 complete; 4+5 = 3/4–almost complete; 6 = full breeding plumage. There are significant differences in the progress of pre-nuptial moult among plumage categories (Kruskal-Wallis  $H = 11.84$ , 3 d.f.,  $P = 0.008$  adjusted for ties).

Dorsal plumage colour	Pre-nuptial moult score					Mean moult score $\pm$ S.E.
	0	1	2+3	4+5	6	
1 ( <i>spoliator</i> )	14	2	3	2	0	0.86 $\pm$ 0.29
2	20	12	18	9	1	1.71 $\pm$ 0.22
3	17	14	24	8	2	1.80 $\pm$ 0.19
4 ( <i>lathamii</i> )	1	1	4	3	1	2.90 $\pm$ 0.56



**FIG. 6.** Relationship between testis size (length of longest axis in mm  $\pm$  S.E.) and dorsal plumage colouration among male Red-billed Queleas sampled during pre-migratory fattening in Zimbabwe, Bulawayo. 1 = *spoliator*-type individuals; 2 and 3 are intermediate; 4 = *lathamii*-type individuals. There is a significant association between plumage score and testis size (one-way ANOVA:  $F = 4.43$ , 3 d.f.,  $P = 0.005$ ), with *lathamii* (category 4) being significantly larger than the others (Tukey's multiple comparison).

two extremes of a continuous variation in colour. Examination of museum specimens revealed that almost the entire range of dorsal colouration occurs among specimens referred to both taxa, including paratypes of *spoliator*. Similar variation occurred among non-breeding birds sampled together in the wild: the majority were intermediate in dorsal plumage colouration while the typical states for *lathamii* and *spoliator* were relatively scarce. Significantly, breeding males whose dorsal plumage scores spanned the range between *spoliator* and *lathamii* occurred together in the same colonies.

More persuasive morphological evidence of separation into *spoliator* and *lathamii* would be a clear difference in the colour-morph frequencies of males in breeding plumage, although this character may be less clearly diagnostic of the accepted subspecies of *Q. quelea* than previously thought (Manikowski *et al.* 1989). Analyses of the frequencies of facial mask, crown and breast colour-morphs of males in breeding plumage from the supposedly discrete breeding ranges of *lathamii* and *spoliator* yielded equivocal results that showed no consistent association with either taxon and whose biological significance is unknown. Furthermore, this variation in male nuptial colouration, which has provided the basis for distinguishing the subspecies of Red-billed Queleas elsewhere in Africa, shows no association with differences in dorsal plumage colour.

The likely migration patterns of the two taxa suggest no mechanism by which sufficient genetic isolation could be established, unless *spoliator* consistently respond to an earlier onset of the rains in their breeding range by coming into breeding condition significantly sooner than *lathamii*. This did not seem to be the case among the birds studied here. Indeed, contrary to expectation, our data on the timing of pre-nuptial moult and testis development suggest that *lathamii* might come into breeding condition sooner than *spoliator*. The biological significance of this finding is unknown.

There are two other reasons why the two taxa are unlikely to be separated by differences in the timing of breeding. The first is that many supposed *spoliator* evidently move into the breeding range of *lathamii* well before the end of the dry season (Clancey 1973), and so would be expected to experience the next rainfall at the same time as indigenous *lathamii* and respond to it in the same way. The second is that reproductive isolation sufficient for

subspecific separation could be maintained only if the two forms continue to breed in discrete colonies for the whole of the ensuing rainy season, and this seems most unlikely. As the season progresses *lathamii* and *spoliator* would be expected to come into contact elsewhere as they make further itinerant breeding attempts along their breeding migration (Ward 1971). By the time the first breeding attempt is over, suitable conditions for a second are likely to be found mainly within the breeding range of *lathamii* where the rains are later. By this time any temporal or geographical separation between breeding *spoliator* and *lathamii* is likely to have broken down, such that they will come together in the same colonies. Without any behavioural barriers to interbreeding, and none has been proposed, it seems improbable that genetic isolation between *spoliator* and *lathamii* could be maintained.

We conclude, therefore, that because '*spoliator*' individuals cannot be separated from *lathamii* on morphological criteria in either breeding or non-breeding plumage, and because both forms breed in the same places at the same times, the subspecies of Red-billed Quelea *spoliator* does not reflect any meaningful phylogenetic division. The Red-billed Quelea should therefore be regarded as being represented by subspecies *lathamii* alone in southern Africa.

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## APPENDIX IA

Specimen numbers of Redbilled Queleas obtained on loan from the Durban Natural Science Museum. Paratypes of *Q. q. spoliator* are marked with an asterisk. Dorsal plumage scores (see text) assigned independently by R.A.C. and M.D., respectively, are given in brackets.

*Q. q. lathamii*: 10867 (3,3); 10868 (2,3); 10869 (3,3); 10870 (3,3); 10871 (4,4); 10873 (3,2); 10874 (3,2); 10875 (3,3); 10877 (1,2); 10878 (2,2); 10879 (1,2); 10880 (2,3); 10881 (3,3); 10882 (2,4); 10883 (2,2); 10884 (2,2); 10885 (1,2); 16714 (4,4); 20108 (2,4); 21961 (3,4); 25561 (4,4); 25671 (4,3); 25672 (3,4); 25673 (3,4); 30615 (3,3); 31586 (1,2); 31587 (2,2); 31588 (3,3).

*Q. q. spoliator*: 10891\* (2,2); 10892\* (3,3); 10893\* (2,2); 10894\* (1,2); 10895\* (2,2); 10896\* (2,2); 10897\* (2,3); 10898\* (3,3); 10899\* (1,2); 10901 (1,2); 10902 (1,2); 10903 (1,2); 10904 (3,3); 10905 (1,2); 10906 (2,3); 10908 (2,2); 10909 (1,1); 10910 (1,2); 10911 (3,3); 10912 (3,3); 10913 (2,2); 21308 (1,2); 21963 (2,4); 21964 (3,3); 21965 (2,4); 21966 (2,3); 21967 (3,3); 21968 (1,2); 21969 (1,2); 21970 (2,2); 21971 (1,3); 24396 (2,2); 24397 (3,4); 26177 (2,3); 26178 (2,3); 27564 (3,3); 27956 (3,4); 28213 (2,3); 28217 (2,2); 28219 (2,2); 28220 (3,3); 28222 (2,3); 28223 (3,2); 28231 (4,4); 28232 (2,2); 28233 (2,4); 28234 (2,2); 28235 (2,3); 28236 (2,2); 36960 (1,1).

## APPENDIX IB

Specimen numbers (NM No.) of Redbilled Queleas, identified to subspecies by P.A. Clancey, held in the Natural History Museum of Zimbabwe. Dorsal plumage scores assigned by consensus between R.A.C. and P.J.J. are given in brackets.

*Q. q. lathamii*: 8415 (4); 11701 (4); 11702 (4); 27980 (2); 28254 (3); 28255 (3); 31279 (4); 36881 (3); 36882 (3); 36884 (4); 36889 (3); 36890 (4); 36892 (4); 36893(4); 36894 (3); 36895 (4); 36896 (3); 36897 (3); 36898 (4); 60174 (3); 67376 (3); 69113 (4); 13134–126 (3).

*Q. q. spoliator*: 8544 (3); 10338 (1); 10339 (2); 11379 (3); 16848 (3); 18189 (2); 23059 (2); 23060 (1); 23067 (1); 37411 (2); 54259 (2); 58289 (3); 63163 (3); 69117 (3); 70759 (2); 72273 (2); 76370 (2); 13134–134 (1).