

# A comparative analysis of movements of southern African waterfowl (Anatidae), based on ringing recoveries

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A total of 2 137 recoveries of nine species of waterfowl ringed in southern Africa were analysed for information on movement patterns. No spurwinged geese *Plectropterus gambensis* and very few yellowbilled duck *Anas undulata*, South African shelduck *Tadorna cana* and Egyptian geese *Alopochen aegyptiacus* had travelled over 1 000 km, with the former two species dispersing markedly shorter distances on average than the latter pair. By contrast, more than 5% of recoveries of redbilled teal *Anas erythrorhyncha*, Cape teal *A. capensis*, southern pochard *Netta erythrophthalma* and knob-billed duck *Sarkidiornis melanotos* had moved over 1 000 km. Redbilled teal travel widely within southern Africa, but rarely far beyond, whereas median distance of movement by southern pochard is far greater, with numbers of birds reaching East Africa. Median movement of Cape teal is the lowest of any species, but some individuals are nomadic over considerable distances within southern Africa. Knob-billed duck are pronounced partial migrants, with nearly 10% of recoveries having moved over 2 000 km and some birds reaching north-central Africa. The subspeciation patterns of these eight species correlate closely with the extent of movement revealed by ringing recoveries. Limited recoveries available for the ninth species, the whitefaced duck *Dendrocygna viduata*, indicate only very limited movements, but other evidence, including its lack of subspeciation over a huge world range, strongly suggests that a proportion of individuals in fact travel extensively.

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'n Totaal van 2 137 terugvindings van nege soorte eende wat in suidelike Afrika bering is, is ontleed vir informasie oor bewegingspatrone. Geen wildemakou *Plectropterus gambensis* en baie min geelbekeend *Anas undulata*, kopereend *Tadorna cana* en kolgans *Alopochen aegyptiacus* het meer as 1 000 km afgelê; die eersgenoemde twee soorte het deur die bank opvallend oor korter afstande versprei as die laaste twee. In teenstelling het meer as 5% van terugvindings van rooibekeend *Anas erythrorhyncha*, teeleend *A. capensis*, bruineend *Netta erythrophthalma*, en knobbeleend *Sarkidiornis melanotos* oor meer as 1 000 km beweeg. Rooibekeende reis ver binne, maar selde ver buite suidelike Afrika, terwyl mediane bewegingsafstande van die bruineend veel groter is, en talle voëls Oos-Afrika bereik. Mediane bewegingsafstande van die teeleend is die laagste van enige soort, maar sommige enkelinge is nomadies oor aansienlike afstande binne suidelike Afrika. Knobbeleende is beslis gedeeltelik swerwers; bykans 10% van die terugvindings het meer as 1 000 km getrek en sommige voëls het noordelike sentraal-Afrika bereik. Die subspecies-patrone van hierdie agt soorte korreleer goed met die bewegingsomvang blootgelê deur ringterugvindings. Beperkte terugvindings beskikbaar vir die negende soort, die nonnetjie-eend *Dendrocygna viduata*, dui aan dat hulle bewegings baie beperk is, maar ander bewyse, insluitende die gebrek aan subspecies oor 'n wêreldwye verspreidingsgebied, dui sterk daarop dat enkelinge wel op groot skaal rondbeweeg.

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## Introduction

Sixteen species of African Anatidae breed in southern Africa (*sensu* Clancey 1980). Although all of these species have been ringed, some in their thousands, by Nature Conservation research staff in the Transvaal, Orange Free State and Cape Province, and in Zimbabwe, our knowledge of their movement patterns bears relatively poor comparison with what is known of waterfowl in Europe and North America (Milstein 1975; Siegfried 1970). Over 50 recoveries away from the place of ringing were available in June 1984 for the following species: whitefaced duck *Dendrocygna viduata*, Egyptian goose *Alopochen aegyptiacus*, South African shelduck *Tadorna cana*, yellowbilled duck *Anas undulata*, Cape teal *A. capensis*, redbilled teal *A. erythrorhyncha*, southern pochard *Netta erythrophthalma*, knob-billed duck *Sarkidiornis melanotos* and spurwinged goose *Plectropterus gambensis*. The aim of the present paper is to provide a quantitative, comparative analysis of the overall movement patterns of these nine species, as revealed by ringing recoveries.

Subsets of the recoveries available for most of the species considered here have been analysed previously, but such studies have either related solely to birds ringed and/or recovered within restricted areas of southern Africa or have been based on relatively small samples and are now considerably out of date. By far the major waterfowl ringing centre in southern Africa is at Barberspan (26°33' S/25°36' E) in south-western Transvaal, and relatively recent discussions of recoveries of waterfowl ringed there have been published (Milstein 1975; Dean 1977). Similarly, Colahan (1984) has provided detailed documentation of the very limited waterfowl recovery data relating to Natal. Winterbottom (1964, 1968) mapped recoveries of redbilled teal and yellowbilled duck ringed in South Africa, and McLachlan (1964) did the same for redbilled teal and South African shelduck; a more recent analysis of shelduck recoveries relating to the Orange Free State has been provided by Geldenhuys (1979). Finally, Siegfried (1967) reviewed movements of both shelduck and Egyptian geese ringed during the mid 1960s at Vogelvlei (33° 22' S/19°03' E), south-western Cape. None of these studies provided any comprehensive, quantitative analysis.

## Methods

A total of 2 137 recoveries involving movement away from place of ringing was available in the SAFRING data bank in June 1984 for the nine species under consideration; this amounted to slightly over 2% of the estimated total numbers of these species which had been ringed. Sample sizes for individual species ranged between 54 and 753 (Table 1). The

**Table 1** Movement statistics for nine species of waterfowl ringed in southern Africa

Species	No. of recoveries	Median distance (km)	98% distance (km)	Maximum recorded movement (km)	Ratio of 98%: median distance	$r^a$
Whitefaced duck	54	99	463	609	4,7:1	0,35
Spurwinged goose	136	142	571	612	4,0:1	0,54
Yellowbilled duck	753	128	607	1 007	4,7:1	0,55
South African shelduck	328	249	987	1 075	4,0:1	0,73
Egyptian goose	329	204	1 001	1 164	4,9:1	0,72
Redbilled teal	269	244	1 607	2 191	6,6:1	0,80
Cape teal	68	54	1 649	2 171	30,5:1	+
Southern pochard	123	724	2 955	3 158	4,1:1	0,87
Knob-billed duck	77	187	3 649	3 880	19,5:1	+

<sup>a</sup>Mean proportion of birds moving beyond each 100-km zone. + Not calculated (see text).

SAFRING computer program provided great-circle distances between ringing and recovery sites of each bird, from which both the median distance of movement and the distance incorporating 98% of all movements (hereafter referred to as the '98% distance') were calculated for each species. In subsequent analyses, 98% distance, rather than maximum recorded movement, was used to quantify extreme movement for two reasons: first, it is relatively independent of sample size; secondly, it facilitates calculations involving logarithmic transformations.

The recoveries for each species were grouped into notional zones, each 100 km wide, radiating out from the place of ringing. From this, the percentages of recoveries within and beyond successive zones were plotted against distance for each species, providing a graphical relationship in which the steepness of the curve is directly related to the proportion of available birds which remain within each successive zone. For each species for which the overall relationship was not systematically curvilinear, the mean proportion of birds moving beyond each 100-km zone ( $r$ ) was calculated, using the equation

$$r = 1 - \frac{N}{\sum jd_j}$$

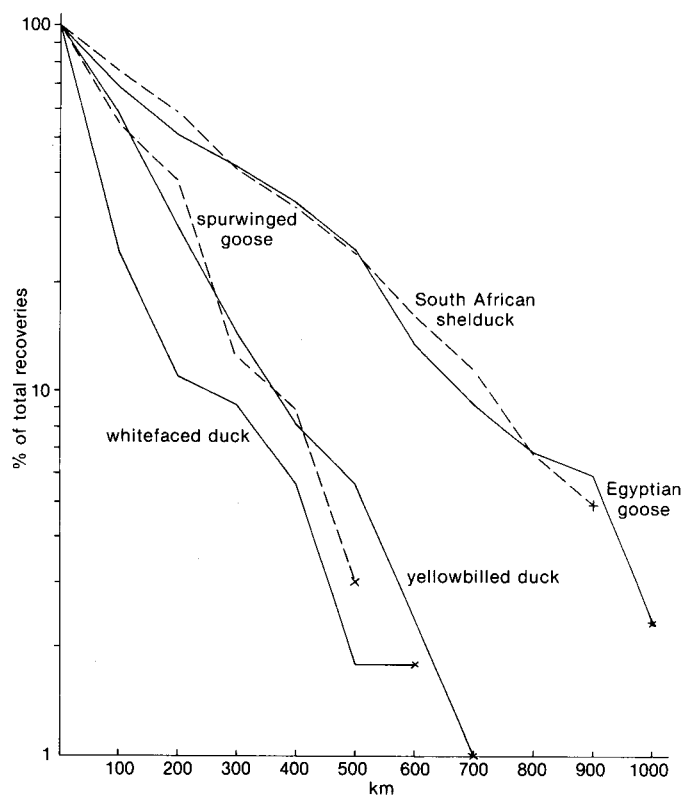
where  $N$  is the total number of recoveries and  $d_j$  is the number recovered in zone  $j$  (cf. Coulson & Brazendale 1968). Finally, for species in which more than 5% of recoveries exceeded 1 000 km, these movements were mapped individually.

## Results

Median distance of movement, 98% distance, and maximum recorded movement are presented for each species in Table 1. Median distance varies by more than an order of magnitude among the species, but is not significantly correlated with either 98% distance ( $r = 0,52$ ,  $d.f. = 7$ ,  $P > 0,1$ ) or maximum recorded movement ( $r = 0,47$ ,  $d.f. = 7$ ,  $P > 0,1$ ), implying substantial inter-specific differences in the distribution patterns of recoveries. For a hypothetical species in which the log percentages of recoveries within and beyond successive zones from place of ringing declined precisely linearly with increasing distance, the ratio of 98% distance to median distance would be 5,6:1. The movements of seven species approximate to this ratio, but those of the remaining two, i.e. Cape teal and knob-billed duck, depart radically from it (Table 1), the medians in both cases being markedly low relative to the 98% distances.

The movement patterns of the five species in which either no individuals or very few (< 5%) had recorded movements

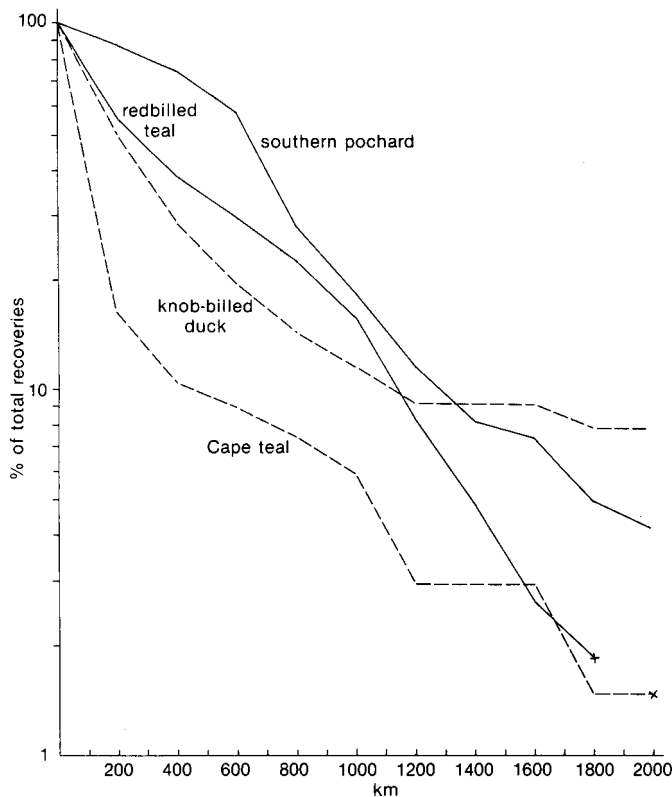
exceeding 1 000 km are shown in Figure 1. The log percentage recoveries of spurwinged goose, yellowbilled duck, South African shelduck and Egyptian goose within and beyond successive 100-km zones from their ringing places all exhibit an approximately linear fall-off with increasing distance. These species nevertheless separate clearly into two pairs, i.e. the spurwinged goose and yellowbilled duck on the one hand and the South African shelduck and Egyptian goose on the other, with the former pair having markedly more restricted movements than the latter (Table 1). Available data for the whitefaced duck indicate it has the most restricted movement pattern of those shown in Figure 1, with the lowest proportion of birds moving beyond each 100-km zone (Table 1). However, the data for this species must be treated with caution, both because the sample size is the smallest for any species and because over 25% of available recoveries represent movements between a single ringing site in Zimbabwe and



**Figure 1** Percentages of recoveries of five species of duck within and beyond successive 100-km zones from place of ringing. x—falls below 1% in next zone.

a recovery area 99 km distant where whitefaced ducks happened to be shot frequently.

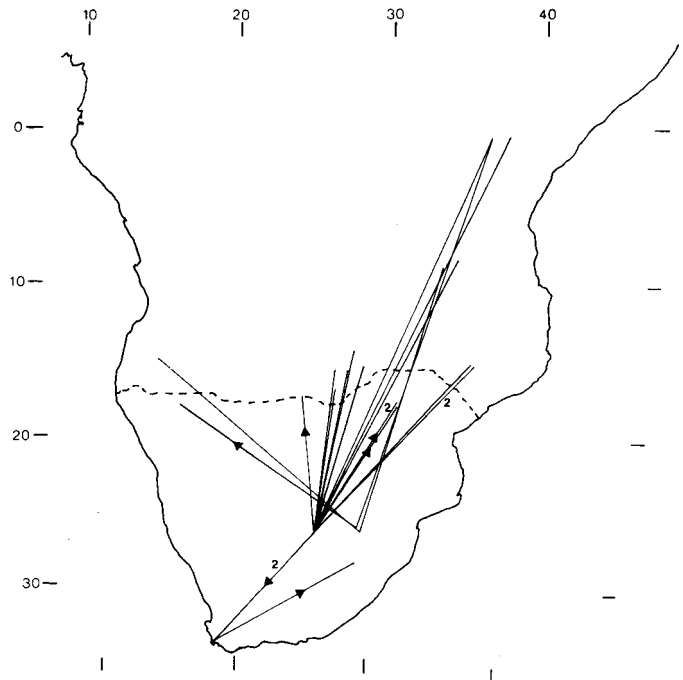
The movement patterns of the remaining four species, in all of which more than 5% of recoveries had travelled over 1 000 km, are shown in Figure 2. Those of the redbilled teal



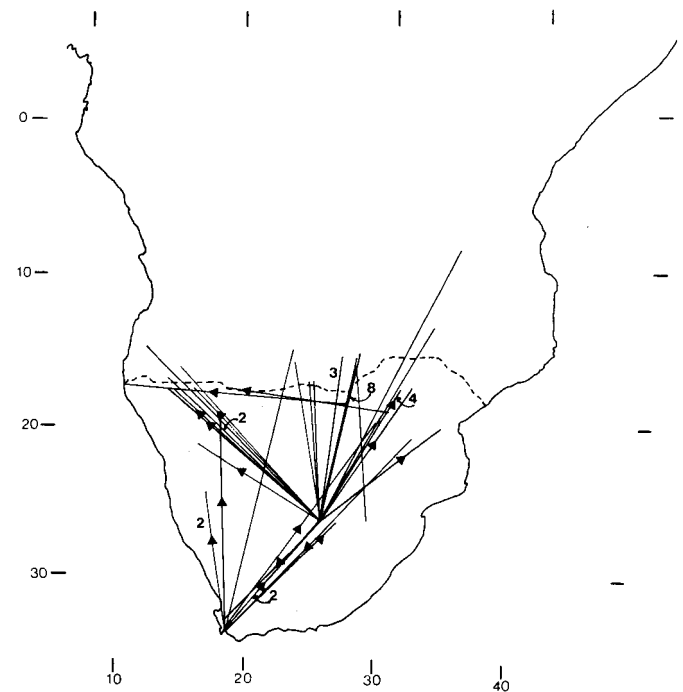
**Figure 2** Percentages of recoveries of four species of duck within and beyond successive 200-km zones from place of ringing. x—falls below 1% in next zone. (N.B. Different abscissa scale from Figure 1, with data plotted at 200-km intervals.)

and southern pochard approximate in very broad terms to a linear fall-off in numbers with increasing distance, with the mean proportion of birds moving beyond each 100-km zone being considerably greater in the case of the southern pochard (Table 1). The main departures from a linear pattern of fall-off with distance in the two species differ: whereas the redbilled teal has a relative underrepresentation of recoveries at intermediate distances (500–1 000 km), the southern pochard exhibits a marked peak in recoveries, comprising  $\approx$  25% of the total sample, in the 701–800-km zone. This peak is almost entirely caused by pochard ringed at Barberspan which moved east before being killed at or near Lake Chuali (25°00' S/32°55' E), southern Mozambique, which was formerly a popular shooting area close to that country's capital city. The 98% and maximum distances of movement of the southern pochard are second only to those of the knob-billed duck, and its median distance of movement far exceeds that of any other species (Table 1). A map of pochard movements exceeding 1 000 km shows that around 5% of all recoveries had moved up into east Africa, some going almost to the equator (Figure 3). By contrast, almost no southern African redbilled teal move far outside the region, although within it they travel widely (Figure 4).

As implied by their very high ratios of 98%:median distance (Table 1), the movement patterns of the Cape teal and the knob-billed duck depart radically from a linear fall-off with

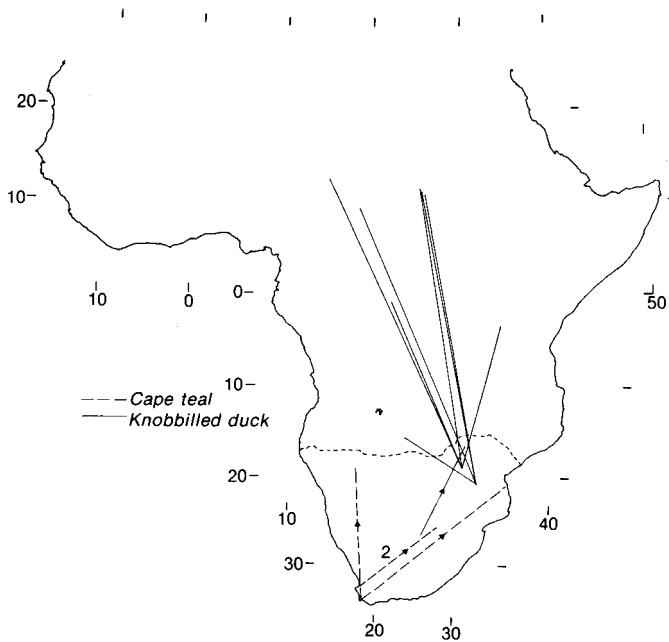


**Figure 3** Map of recoveries of southern pochard which moved more than 1 000 km from their place of ringing. Arrows show direction of movement of birds recovered within southern Africa. Numbers indicate that more than one recovery had undertaken the same movement.



**Figure 4** Map of recoveries of redbilled teal which moved more than 1 000 km from their place of ringing. Conventions as for Figure 3.

increasing distance (Figure 2). Instead, for both species they follow a pronounced concave curve; as a result, calculation for either of a mean proportion of birds moving beyond each 100-km zone is not informative. Although the basic pattern of movement is not dissimilar between the two species, both median and maximum distances travelled by the Cape teal are very much lower (Table 1). The furthest recovery recorded for Cape teal had travelled only slightly in excess of 2 000 km, and the limited number of available long-distance (> 1 000



**Figure 5** Map of recoveries of Cape teal and knob-billed duck which moved more than 1 000 km from their place of ringing. Conventions as for Figure 3.

km) recoveries indicate that southern African birds travel little, if at all, outside the region (Figure 5). By contrast, nearly 10% of knob-billed ducks had travelled over 2 000 km, with recoveries from well north of the equator, at distances exceeding 3 500 km, predominating among these (Figure 5).

### Discussion

The study reported here is a comparative overview in which the potential roles of age, sex, geographical area, season, and inter-year variation of climate in affecting movement patterns within the different species have not been considered, largely because the available data were inadequate to do so in any systematic manner. Similarly, geographical biases in probability of recovery have been alluded to only in particular instances in which their operation appeared most clear-cut. Nevertheless, while bearing in mind that the results presented carry no implications regarding the purpose or timing of any movement, a broad outline of similarities and differences among the various species has emerged which we consider to be biologically interesting.

As the relevant maps in Maclean (1985) indicate, none of the species under consideration completely vacates any part of its southern African breeding range. Such movements as occur involve dispersal, partial migration and nomadism. Use of the terms 'dispersal' and 'dispersive' here implies merely that the proportional fall-off in recoveries with increasing distance remains roughly constant, i.e. by simple linear extrapolation it is possible approximately to predict the pattern of the more extensive movements from a knowledge of those nearer the point of ringing (*cf.* Coulson & Brazendale 1968). Reference to dispersal may thus incorporate phenomena such as the tendency of certain species, e.g. South African shelduck and Egyptian goose, to undertake local 'moult migrations', in which birds congregate from scattered breeding localities onto larger water bodies before moulting.

In terms of the main parameters of distance and pattern considered, the yellowbilled duck and spurwinged goose emerge as having extremely similar, relatively restricted dispersals. Similarly, the South African shelduck and Egyptian

goose form another pair of dispersive species, distinguished from the former two by virtue of their more extensive movements. The close similarities within these pairs of species have not previously attracted comment, but the results do tend to confirm the generally held view, most recently summarized by Benson (1982), that none of these species can be considered migratory. The dissenting opinion of Curry-Lindahl (1981, p. 377) that the yellowbilled duck is highly migratory is unsupported for southern African birds, even allowing for the broad and vague definition of the term migration that he uses (p. ix), and his comments regarding the migratory or partially migratory status of other species are largely unhelpful in any sense other than as an indication that movement occurs. In fact, all four of the species above show ratios of 98%:median distance below the 5,6:1 expected for a dispersal in which the distribution of suitable habitats is not biased in terms of distance, implying a tendency towards truncation of movements further than their respective medians.

It has long been appreciated that movements by the redbilled teal tend to be greater than those of the yellowbilled duck (McLachlan 1964; Winterbottom 1964), and the results here bear this out. Furthermore, the map of the redbilled teal's longer distance recoveries is in good accord with Douthwaite's (1977) concept of a single, mobile population in southern Africa. However, it remains an open question whether its movements are better viewed as strongly dispersive (*cf.* Benson 1982) or partially migratory (Douthwaite 1977). Notwithstanding the recent (1982) recovery in Tanzania of a single bird ringed at Barberspan, Irwin (1981, p. 51) rightly contrasted the minimal mixing of southern and eastern African populations of redbilled teal with the much greater degree of movement of southern pochard and knob-billed duck beyond the borders of the South African subregion. Benson (1982) considered that confirmation was needed as to whether the last two species were to some extent migratory, and not merely dispersive. The present study provides this confirmation for the knob-billed duck, in which a percentage of the population is clearly migratory. However, the data for the southern pochard are insufficient and contain too many probable biases to examine conclusively the idea, originally advanced by M.K. Rowan (in Winterbottom 1964), of a migratory component in its South African population.

The evidence adduced in favour of a migratory or, more probably, nomadic tendency among a proportion of Cape teal can now be seen as having been foreshadowed by the brief comments of Winterbottom (1974, p. 117). However, the species was not mentioned by Benson (1982), although Taylor (1982) considered that the appearance of individuals in northern Zambia supported the concept of long-range movements from southern areas. Ringing recoveries for the final species, the whitefaced duck, indicating that its movements are very restricted, are paradoxical. Whereas the species is present throughout the year over its range in southern Africa (Clark 1974; Irwin 1981; Colahan 1984) and adjacent areas (Douthwaite 1977), its numbers tend to fluctuate considerably and it is the only species among those considered here that is known as an extralimital vagrant to the Seychelles (Prÿs-Jones, Prÿs-Jones & Lawley 1981; Feare & Watson 1984). A total discrepancy of opinion emerges from the two major recent reviews of migration in southern Africa. Benson (1982) fails to mention the species at all, whereas Curry-Lindahl (1981, p. 240) refers to considerable migrations and suggests (p. 270) that some birds move across the equatorial forest regions into north-central Africa, i.e. a migration as great as that under-

**Table 2** Numbers and distributions of subspecies of the nine species of waterfowl, in relation to their 98% distance of movement

Species	98% distance (km)	No. of subspecies	Distribution of subspecies
Whitefaced duck	463	1	Sub-saharan Africa; Madagascar; central and south America.
Spurwinged goose	571	2	(i) Sub-Saharan Africa north of <i>ca</i> 15°S. (ii) Sub-Saharan Africa south of <i>ca</i> 15°S.
Yellowbilled duck	607	2	(i) Ethiopian highlands. (ii) Sub-Saharan Africa south of <i>ca</i> 5°N.
South African shelduck	987	1	Sub-Saharan Africa south of <i>ca</i> 20°S.
Egyptian goose	1 001	1	Sub-Saharan Africa and the Nile Valley.
Redbilled teal	1 607	1	Sub-Saharan Africa, exclusive of western, and parts of central, Africa; Madagascar.
Cape teal	1 649	1	Sub-Saharan Africa, exclusive of western and central Africa.
Southern pochard	2 955	2	(i) Sub-Saharan Africa, exclusive of western and central Africa. (ii) South America.
Knob-billed duck	3 649	2	(i) Sub-Saharan Africa; Madagascar; southern Asia, from Pakistan east through Indochina. (ii) South America.

taken by some knob-billed ducks. Large numbers of whitefaced duck are also known to congregate at times on wetlands in west-central Africa (Roux & Jarry 1984). Independent evidence considered below suggests that Curry-Lindahl's ideas may well be much closer to the truth, and that ringing recoveries to date provide an inadequate and distorted picture of the species' movements.

Using information derived from Johnsgard (1979), Table 2 summarizes the numbers and distributions of subspecies within each of the nine species under consideration, the species being listed in order of increasing 98% distance of movement. Neglecting for the time being the whitefaced duck, a clear relationship between pattern of subspeciation and 98% distance of movement emerges from this. Species having short-distance movements (<< 1 000 km) show a distribution restricted to sub-Saharan Africa and more than one subspecies within this area. Species with intermediate movements (*ca.* 1 000–2 000 km) similarly show a distribution limited to sub-Saharan Africa (including Madagascar in the case of the redbilled teal), but only a single subspecies within this area. Species having long-distance movements (> 2 500 km) show a distribution extending greatly outside sub-Saharan Africa and involving more than one subspecies, but with only one occurring within sub-Saharan Africa. In the case of the knob-billed duck, which has the greatest recorded movements of any species under consideration, the African subspecies additionally occurs throughout southern Asia.

On the basis of this striking covariation of 98% distance of movement and subspeciation pattern, a reasonable prediction for a species with the very limited recorded movements of the whitefaced duck would be that it would have a strictly sub-Saharan distribution involving two or more subspecies. In fact, the truth could not be more different: it has an African, Malagasy and southern American distribution involving only a single subspecies. In the light of the independent conclusions of Curry-Lindahl (1981), mentioned above, it appears highly probable that a proportion of whitefaced ducks undertake extensive movements which ringing recoveries have thus far failed to reveal. As such, the species should be viewed as a prime subject for ringers wishing to make a material contribution to our understanding of the movements of southern African waterfowl.

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