Range expansion of the hadeda ibis *Bostrychia hagedash* in southern Africa

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The southern African range of the hadeda ibis *Bostrychia hagedash* has expanded from 530,900 km² in 1910 to 1,323,300 km² in 1985. Major range expansions have occurred in the fynbos biome of the south-western Cape, the Karoo, the grasslands of the eastern Cape, the Orange Free State and the Transvaal highveld. Smaller expansions are documented for Lesotho, eastern Zimbabwe, central Mozambique and westwards along the Zambezi, Okavango, Limpopo and Orange rivers. The reasons for this expansion were investigated. Important factors include reduction in human persecution following the introduction of legislation in the period 1934 to 1941 and an increase of alien trees in formerly treeless areas. The increases in artificial impoundments and areas under irrigation are thought to have played a smaller role.


Extensions in the range of the hadeda ibis *Bostrychia hagedash* (hereafter called the hadeda) have been recorded since 1910 from numerous, widely scattered localities in southern Africa (e.g. Davies 1911; Helme 1932; Skead 1951, 1967; Forrester 1966; Plowes 1967; Winterbottom 1972; Bonde 1981; Collett 1982; Uys 1983). Although this range expansion has been noted in several recent accounts of the southern African avifauna (e.g. Snow 1978; Brown, Urban & Newman 1982; Maclean 1985), there has been no detailed investigation of the phenomenon. Skead (1966) documented the situation in the eastern Cape Province and concluded that the expansion was probably the result of a population build-up in its original distribution range. Vernon (1972) suggested that the range expansion has occurred in response to modifications in the southern African environment brought about by agriculture. He details these modifications as ‘an increase in available water, the clearing of scrub vegetation, the provision of trees in which to nest where none existed before, and farm lands to feed in’. He suggests that the hadeda has benefited particularly from artificial irrigated pastures grown for dairy cows (Vernon 1972). Snow (1978) and Brown *et al.* (1982) give the construction of water storage impoundments as the reason for the range expansion.

In this account we document the range expansion that has occurred since 1910 and then investigate a series of hypotheses that can be erected to explain it.

**Methods**

Establishing the range of the hadeda

Distribution records were obtained mainly from the southern African ornithological literature. In particular the journals Bokmakierie, Honeyguide, Ibis, Journal of the South African Ornithological Union, Koedoe, Ostrich, The South African Avifauna Series, The South African Journal of Natural History and Southern Birds, were scanned for hadeda records. Newsletters of some branches of the Southern African Ornithological Society (SAOS) and other ornithological societies were also scanned, i.e. Babbler, Bee-Eater, Diz Bird Club News, Wits Bird Club Newsletter and Promerops. For early distribution records we referred to the published accounts of several pioneering naturalists (e.g. Sparrman 1786; Barrow 1801; Livingstone 1857; Gurney 1865; Layard 1867; Ayres 1871; Anderson 1872; Buckley 1874; Woodward & Woodward 1875, 1899; Layard & Sharp 1884; Shortridge 1904; Stark & Slater 1906; Slater 1912; Roberts 1936; Dobie 1945; Lugg 1970; &folliot & Liveridge 1971; Krauss 1973).

For more recent distribution records, the published or unpublished results of several regional bird atlas projects were

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consulted (e.g. Tarboton 1968; Cyrus & Robson 1980; Kemp, Kemp & Tarboton 1985; Cape Bird Club in prep.; National Museum, Bloemfontein in prep.; Botswana Bird Club in prep.; South West African Directorate of Nature Conservation in prep.). In addition, unpublished records were obtained from the Nest Record Card collection of the SAOS, from the authors’ own files and from those of several other ornithologists (see Acknowledgements).

Only those records that could be accurately located to a locus (= 'quarter-degree square') (Boshoff, Brooke & Crow 1978) were accepted. The only exception to this rule was information from the Botswana Bird Club atlas project where the distribution is mapped by 'half-degree squares'. In this case the four included loci were all recorded as having the same state as the half-degree square, i.e. hadedas present or absent. This may have exaggerated the Botswana range of the hadeda in the map of its recent distribution. Generalized statements on the distribution range were not mapped.

Whenever a record was stated to be the first recorded sighting of the species from a locality where observations had been made over an extended period of years before the observation, the date of this first record was mapped. These first records were grouped into the periods 1911 to 1969, 1970 to 1979, and 1980 to 1985 in the final map. Records were accepted only up to the end of 1985.

From those accounts of local avifaunas that did not include the hadeda, a 'negative' distribution map was drawn up. In each case the final year of the period during which the avifauna had been compiled was marked on the map. In the case of a conspicuous and well-known species such as the hadeda, the use of these negative records is considered justified. Using both the recorded first sightings and these negative records, it was possible to draw up a range expansion map with limits at the end of the years 1910, 1930, 1955, 1970 and 1985.

Investigating possible explanations for range expansions

In order to test the hypothesis that it is the increase in trees in the formerly treeless portions of southern Africa that has given rise to the observed range expansion, the following approaches were adopted.

Firstly, all the nest records for the hadeda in the SAOS nest record card collection were classified as to whether the nest was in an alien or an indigenous tree. The frequency of records in each class of tree was summed for the area occupied by hadedas up to 1910 and for the area colonized since 1910. These frequencies were arranged in a 2 × 2 contingency table and tested using the chi-squared test.

Secondly, the area of the hadeda's range in the Cape Province (with the boundaries as defined at 1950 and thus incorporating the Transkei) was measured for 1910, 1930, 1955, 1970 and 1976 and compared with the area of plantations of introduced Pinus and Eucalyptus species (the major timber species planted in the Cape) as determined at five-yearly intervals since 1920 (Annual Reports of the Forestry Department, 1920 to 1985).

The possible importance of artificial impoundments as nesting sites was investigated using the SAOS nest record cards. Whenever this factor was recorded on a card, the location of a nest over a river, over an impoundment or over the ground was noted. The frequencies of records of nests over these substrata were compared for the pre-1910 and post-1910 range of the hadeda using the chi-squared test.

The role of irrigation in promoting the spread of the hadeda was investigated by comparing the area occupied by the species in the Cape Province with the area of irrigated farms and the total area under irrigation in the province as recorded by the Directorate of Agricultural Economic Trends (1985) and the Agricultural Census (Office of Census and Statistics, Pretoria).

Results and Discussion

Distribution before 1910

All the hadeda records that could be accurately located for the period up to and including 1910 are plotted in Figure 1. Unfortunately this cannot be taken as being indicative of the distribution range of the species under pristine conditions. Even at this stage there were indications that the hadeda was extending its range in response to man-made changes in the environment. For example, at Modderfontein (2628CB) on the Transvaal highveld the species had not been recorded by 1902 (Haagner 1902) but by 1905 a single immature male had been collected there (Haagner 1905). In his introduction Haagner (1905) mentions that the creation of plantations and artificial impoundments had been 'responsible for a considerable number of additions to the local avifauna . . . within the last few years'. At about this time, the species was still not present in the adjacent areas of Irene (Taylor 1906) and Johannesburg (Haagner 1902). Although recorded in the 1830s from along the Vaal River where this traverses the Transvaal highveld (Arbousset & Daumas 1846), the species was considered 'very scarce' here (Ayres 1871). It was not recorded by Holub during the 1870s in his extensive exploration of the Vaal River west of Potchefstroom and of the Harts and upper Limpopo catchment (Holub & Von Pelzeln 1882). Even in the Natal midlands there is a record that indicates that the bird's presence might have been influenced by man before 1910: Clarke (1904), reporting on six months' observations near Ingogo (2729DB), records that 'a few of these birds used to feed in some plantations of Australian wattles'. Whether the species would have been present in the absence of these plantations is not certain. Just south of the Natal midlands, the species is recorded as colonizing the Kokstad (3029CB) area in the early 1920s. In this locality 'the increase in trees in an otherwise open grassveld district might have helped the increase' (Skead 1966). Thus there are some indications that the hadeda's distribution limits in both the Transvaal highveld and the Natal midlands might already have been expanding before 1910.

The only early record for the interior of the Cape Province is that of Barrow (1801) from the 'plains of the Seacow River' (i.e. the modern Colesberg district at 3025AC). Whether or not this is the correct locality is open to doubt (Skead 1966). Certainly Layard (1867), Layard & Sharpe (1884), Wood (1896), Whitehead (1903) and Stark & Sclater (1906) give no indication that the hadeda occurred in the upper Orange River catchment before 1910.

All the remaining Cape records are for the coastal strip east of Knysna. Even in the coastal districts of the eastern Cape, the species was apparently very localized and generally uncommon at this date. Holub failed to record it anywhere in his journey from Port Elizabeth up to Cradock (Holub & Von Pelzeln 1882) and Pym (1909) records it as rare in the King William's Town district, apparently making only two sightings of the species in the period 1902 to 1908. The accounts of Godfrey (1927, 1928, 1931, 1934) indicate that, even by the 1990s, the species was neither abundant nor generally distributed in the eastern Cape and Transkei.

Further north in the subcontinent, the only record for the
northern interior of the Transvaal is that of Thomsen (1907) who gives an anecdotal account of a flock comprising 'several hundreds' of birds feeding on locusts in the eastern Springbok Flats (2428DA). Although this record is plotted in Figure 1, we have considerable doubt as to its validity as the plumage description and the account of colonial breeding that accompany this record are both inaccurate. The record was apparently recalled from memory following a more recent identification of a pair of hadedas near Barberton. Even in the eastern lowveld of the Transvaal, the species must have been rare at this time as Rendall (1896) makes no mention of it in his account of 15 months' observations made in the vicinity of Barberton, the Sabi River and the Crocodile River.

The species was apparently fairly common in certain localities in the eastern Transvaal (Taylor 1907; Sclater 1912; Ingle 1914) and was present along the rivers in the adjacent areas of Mozambique (Sparrow 1907; Turner 1907). No records could be located for this period from the Limpopo river or the adjacent areas of South Africa and Zimbabwe. The species was apparently absent from the eastern highlands of Zimbabwe; Swynnerton (1908) recorded them only from the adjacent lowland areas of Mozambique, in the Buzi River valley at Chibabava (2033BC) and at Boka (1934CC).

Hadedas were recorded from the Lake Ngami and Okavango delta areas of Botswana by Anderson (1872) and Wahlberg (Gyldenstolpe 1934) and also from the upper and lower Zambezi Valleys (Livingstone 1857; Alexander 1900; Sclater 1905, 1912).

Range expansions since 1910

The known distribution of the species up until the end of 1985 is plotted in Figure 2. The major areas of range expansion are given below.

South-western Cape

The species was first recorded west of Knysna at George (3322DD) by Skead (1966) and at Oudtshoorn (3322CA) by Winterbottom (1968). Subsequently, the expansion westwards across the Little Karoo was documented by Martin (1972), Winterbottom (1972), and Winterbottom & Winterbottom (1984) while that along the southern coastal strip was recorded by Martin (1971), Currie (1974), Uys (1983) and Richardson (1984). The current atlas project of the Cape Bird Club (in prep.) has recorded the hadeda in most loci south of the Olifants River by the end of 1985 (Figure 2).

The most recently occupied areas are around Hopefield (3218CD) and Graafwater (3218BA) (Brooke 1986), the expansion now being northwards up the west coast lowlands. However, on the better watered escarpment at Nieuwoudtville (3119AC) the first sighting was made in 1976 (P. Steyn, pers. comm.).

Karoo

The movement from the Eastern Cape coastal belt into the eastern fringe of the Karoo has been well documented by Skead (1966) and Collett (1982). Subsequent westward penetration of the species into the Karoo proper has been recorded from south of Richmond (3123DB) (Martin 1971), the De Aar area (3023DD) (Kieser & Kieser 1978), the Karoo National Park at Beaufort West (3222AD & BC) (Martin 1984) and from near Sutherland (Kurtz & Mather 1983).
Figure 2 Distribution records for the hadeda, 1911 to 1985. Key: ■ all definite loci without known first arrival dates; ○ loci where the species was first recorded 1911 to 1969; ▼ Loci where the species was first recorded 1970 to 1979; ▲ Loci where the species was first recorded 1980 to 1985; A Loci where the only available record is from one of the recent atlas projects.

Eastern Cape and Transkei
The expansion of the hadeda's range in the eastern Cape has been comprehensively reviewed by Skead (1966). Here the species was recorded as expanding its range in the late 1950s and early 1960s along the coast from the Tsitsikamma Forest westwards as far as George. Hadedas also colonized the inland areas of the eastern Cape, the first indications of the range expansion being in the 1900s but most of the expansion taking place after 1950. At the same time as the expansion occurred a marked increase in the abundance of the hadeda was recorded in its original range (Skead 1966).

Orange Free State and Lesotho
Subsequent to Helme's (1933) first record of the species for the Orange Free State (OFS) at Westminster (2927AA), the hadeda was recorded as becoming more frequent at this locality (Maclean 1957). By 1961, the species had also been recorded from the Bloemfontein, Clocolan, Ficksburg and Winburg districts (Van der Plaat 1961). By 1985, the atlas project had recorded this species throughout most of the province (National Museum, Bloemfontein in prep.).

In Lesotho, Murray (undated) recorded the hadeda as rare in the 1920s, birds being recorded only from the Berea district. By 1963 Jacot-Guillarmod (1963) recorded the species from Leribe, Maseru, Mamathes, Qacha's Nek and Butha Buthe. Quickleberge (1972) obtained the first record of the species for the mountainous interior of the country at Marakabei (2928CA) in 1968. Between 1978 and 1980 hadedas were recorded frequently in the Sahlaba-Thebe National Park (2929CC) between August and December (Balcomp in Bonde 1981). The frequency of occurrence of the species in the Roma area is shown to have increased from 1964 to 1973 (MacLeay & Aspinwall in Bonde 1981). Bonde (1981) concludes that it has increased in numbers in Lesotho in recent years.

Transvaal
The first published indication of the spread of hadedas in this province after 1910 is the change in status of the species from an early summer visitor to an all-year resident at Belfast (253OCA) in 1942 (Bergh 1942, 1943). The species was still considered rare at Modderfontein over the period 1938 to 1950 (Hallack 1951). Several accounts document its increase in the Johannesburg area in the 1950s (Bauling 1955; Currie 1955; Gautier 1956; Last 1957).

The hadeda was recorded at Klerkskraal (2627AC), west of Johannesburg, in 1951 (Bromley 1952) and on the Mooi River south of Potchefstroom (2627CA or CC) in 1954 (Brandt 1960). In 1959 and 1961 the species visited Barberspan (2625DA) (Farkas 1962). [There is an earlier record made on a day's visit to the pan in 1951 (Prozesky & Campbell 1951) but the significance of the record was apparently not known to the authors of the semi-popular account of this visit and it might be wiser to disregard it.] By the end of 1970 the hadeda was still only a rare vagrant to Barberspan (Milstein 1975), but by 1975 the species was recorded continuously from February to December, was present in flocks of up to seven individuals and had bred in the neighbourhood (Skead & Dean 1977).
On the Vaal River at Vereeniging (2627DB) the hadeda was recorded as having increased from about four birds in 1954 to 30 or more by 1959 (Brown 1959). In the Bloemhof district, the first records were made along the river (2725DD, 2726CA) in 1966 (Skead & Brandt 1968).

By the end of 1984 hadedas in the Transvaal had been recorded in all regions — particularly the eastern highveld and the escarpment rivers. Occurs more locally in the semi-arid western and north western areas, where usually restricted to irrigated areas or the fringes of rivers and dams’ (Kemp et al. 1985).

Northern Cape

The first record from the northern Cape was on the Vaal River (2824DA) in 1966 (Forrester 1966). In 1977 the species was resident on the Vaal River at the Vaalharts Weir and at Warrenton (2824BB) and was recorded for the first time at Hartswater (2724DD), on the Ghaap Plateau near Reivilo (2723DB) and, in December 1976, at Kuruman (2723AD) (I.A.W. Macdonald unpubl.). In 1976 the species was recorded down the Vaal River as far as Schmidtsdrif (2824CA) (J.J. du Plessis pers. comm.) and Gubb (1979) recorded one on the Riet River (2824CD) in 1979, by which time it had already been recorded on the Kimberley golf course (2824DB).

By 1983 the species was present at Augrabies Falls National Park on the middle Orange River (Lamont 1983). The species was not recorded in the Park in December 1984, nor further east on the Orange River at Prieska (2822DD) in January 1985. However, hadedas were still present on the Vaal River just above Schmidtsdrif at Rooipoort (2824CA) in December 1984 (I.A.W. Macdonald unpubl.).

It is not known whether the species has persisted on the Ghaap Plateau. When it was recorded here in the late 1970s the area had just experienced several years of exceptionally high rainfall (Tyson & Dyer 1978) and conditions were unusually favourable for the species in this otherwise semi-arid area.

Botswana

The occurrence of the hadeda along virtually the entire south-eastern border of Botswana by the mid 1980s (Fraser 1982; Botswana Bird Club in prep.) indicates a marked extension of range relative to the mid 1960s when the species had not yet been recorded from anywhere in the country along this border (Smithers 1964).

There are no indications of an expansion of the range of the hadeda (here represented by the subspecies B. h. brevirostris) in the northern portion of Botswana. In this area it is associated with open channels of various swamp and river systems where there is well developed riverine forest (Smithers 1964; Irwin, Niven & Winterbottom 1969). If anything, there is an indication of a slight range contraction at the southern edge of this population’s range. Although recorded from Lake Ngami by Wahlberg in the 1850s (Gyldenstolpe 1934) the species has not been recorded there in recent years (Fraser 1971; Dawson & Jacka 1975). The area is thought to have recently become drier (Smithers 1964; Dawson & Jacka 1975).

South West Africa/Namibia (SWA)

The species is confined to the north-eastern portion of this territory. The distribution in the Caprivi Strip appears to be of long standing. The records made in 1964 at Andara (1821AB) and Mayara (1720CD) west of the Caprivi Strip along the Okavango River were apparently the first ever for SWA proper (Winterbottom 1966). Whether this was due to range expansion or a lack of earlier records is uncertain.

In the 1980s the atlas project has confirmed the restriction of the hadeda to the Caprivi strip. However, two records have been made in central SWA (Figure 2), both single sightings, and their validity has not yet been established (SWA Directorate of Nature Conservation, in prep.).

Zimbabwe and the lower Zambezi Valley

The first definite records for south-eastern Zimbabwe were apparently made only in the 1950s. These were in the Sabi (2032AB and 2132AD) and Lundi (2131BD) valleys in 1950 and 1954 (Pizey 1950; Peters 1954), at the Birchenuough Bridge (1932CD) in 1957 (R.K. Brooke pers. comm.), and at the Bubye-Limpopo confluence (2231AC) in 1958 (Smithers & Hayes 1958). There are no definite indications that these birds were recent immigrants, the absence of previous records probably being the result of the almost total lack of early biological information from this area (Priest 1933). However, the lack of previous records from the well-visited Birchenuough Bridge and the subsequent publication of a 1961 record from here as being unusual (Anon. 1967) indicates that it might have been a recent arrival here. After the construction of several major dams in the catchment of the Lundi River and the creation of large irrigation schemes at Triangle, Hippo Valley and Chiredzi, the hadeda was found breeding at the Esquilingwe Weir (2031CD) in 1966, at Triangle (2131AB) in 1971 and at Hippo Valley (2131BA) in 1975 (SAOS nest record cards). At Hippo Valley it was recorded at the scheme’s effluent disposal pools (Cackett 1974).

There are definite indications that the hadeda subsequently expanded its range westwards up the Limpopo Valley (compare Irwin (1968) and Irwin (1981)) and northwards into the Chipinga area (Plowes 1967; Irwin 1981). The expansion into the upper Buzi River valley (2032BA) within Rhodesia in the period 1967 to 1969 (Plowes 1967; Scott 1972) could have been either eastwards from the Sabi Valley or westwards up the Buzi Valley where it was present about 100 km to the east at the turn of the century (Swynnerton 1908). The species has subsequently become a breeding resident on Buzi Farm (J.A. Scott pers. comm.). By the end of 1979, the hadeda had been recorded at Penhalonga (1832DC) and Stapleford (1832DB) but was not yet resident in these localities (Irwin 1981).

Much confusion surrounds the distribution of the hadeda in the Zambezi valley: Irwin (1981) states ‘present throughout the length of the middle Zambezi Valley and west of the Victoria Falls’. We, however, have not been able to locate any definite records for the Zambezi Valley east of the Victoria Falls (1725DD) and west of Mana Pools (1529CB). Before the construction of Lake Kariba, expeditions failed to record the species from two areas within the Zambezi Valley above the dam wall (Plowes 1955; Rankine 1956). During the filling of the impoundment, an expedition to the Sanyati Gorge area recorded hearing hadeda calling but failed to observe the species (Magness 1959). Donnelly & Donnelly (1983), in their detailed analysis of the pre- and post-inundation avifaunas, make no mention of the hadeda. The species had not been recorded from the area by 1984 (Donnelly 1984). We accordingly reject the Sanyati Gorge sound record as being unconfirmed.

The status of the hadeda below Kariba is also not clear. Cooper (1972), in his checklist of the valley from Kariba (1628DB) to Zumbo (1530CB), states that it is a breeding resident frequenting pans. Smith (1950), however, failed to record the species at Chirundu (1628BB) in four and a half months in 1940. By 1950, there were only three sight records
of this species on the files of the Rhodesian Bird Club — all of single birds recorded in January, one each from the north, south and east of the country (Miles 1950). There were still no records of the species from the Zambezi Valley east of the Victoria Falls by 1959 (Smithers, Irwin & Paterson 1957, 1959). Stoehr did not record the species in a two-year period (July 1903 to July 1905) in the vicinity of Feira (1530CB) (Stoehr & Sclater 1906). The accounts of four recent boating expeditions that have been undertaken along different portions of the river between the Kariba and Caborra Bassa gorges make no mention of this conspicuous bird (Siemers 1964; Rockingham-Gill 1984). The hadeda is also not recorded in accounts of the avifaunas of Chewore Game Reserve (Woodall 1971) and the Dande Communal Lands (Howells 1985) which lie to the east of Mana Pools in the Zambezi Valley. Even in the Lower Zambezi Valley, the species is by no means widespread. Its occurrence here is apparently linked to pan systems rather than to the Zambezi River itself (Hammer 1976).

The first definite record we have been able to trace for the middle Zambezi Valley is that of a pair sighted at Mana Pools (1529CB) in September 1967 (Bradfield 1967). The only other record is of a nest at the same locality in 1978 (SAOS Nest Record Card System). As Mana Pools is relatively well known ornithologically, that the hadeda was first recorded in 1967 is taken here to indicate a possible recent range expansion into this area.

We concur with Clancey (1980) that the lower Zambezi Valley population is discrete from that in the upper valley (B. h. brevirostris in the west and B. h. erlangeri in the east). The absence of the hadeda from most of the middle Zambezi Valley is backed up by the absence of specimens or other records from this area in the map prepared for the 'Atlas of speciation of African non-passerine birds' (Snow 1978).

**Mozambique**

One indication of a possible range expansion of the hadeda in Mozambique comes from the Gorongosa area. Using all the available data to 1957, Pinto (1959) does not list the species for the area; in fact he specifically states that no members of the Plataleidae were recorded. However, in his 1965 list for the area, the species is included (Pinto 1965), and it was common on the Urema floodplain within the National Park in 1969 (Macdonald 1969).

The hadeda is recorded as common in the moist areas just east of the Zimbabwean mountains on Mozambique's western boundary by 1970 (Clancey 1970). Swynnerton (1908) first recorded the species about 100 km east of the border at the turn of the century so that it is possible that this area has also been recently colonized by hadedas.

**Malawi and Zambia**

There are no indications of a range expansion in southern Malawi (Benson & Benson 1977) or southern Zambia (Benson, Brooke, Dowsett & Irwin 1973).

**Angola**

The only possible indication of a range expansion in southern Angola is Pinto's (1983) undated sight record of a flock at Cubalai (1719CD) on the Cubango (= Okavango) River. The hadeda had apparently not been recorded from anywhere in southern Angola before this sighting.

Outside the area of this study, Huntley & Huntley (1974) documented what was apparently a massive range expansion of the hadeda on to the Cuanzo River (0913AB) in 1971. Overall changes in range

The distribution limits of the species at different dates, based on the best available evidence, are plotted in Figure 3. These limits have been based on the presence of the bird rather than on it being resident or breeding at any locality. Presence or absence data are more readily available than status or breeding data. However, evidence from numerous localities shows that the initial recording of a hadeda is almost invariably followed by an increase in frequency of records, increase in the numbers of birds present, the species taking up residence and finally breeding there (e.g. Bergh 1942; Maclean 1957; Skead 1966; Skead & Dean 1977; Richardson 1984; Winterbottom & Winterbottom 1984).

Even when these simple records are used, the pattern of range expansion is often too complex to be accurately reflected in this type of map. In several areas from which numerous first-arrival records are available, e.g. the south-western and eastern Cape, there are sometimes discrepancies of up to 10 years in these dates from different farms within a single locus (see Skead 1966 for examples). There are also a few cases of conflicting accounts from different sources for the first arrival dates at a particular locality. In these cases the date closest to most dates in the surrounding loci has been used. These differences in first-arrival dates are likely to be due to failure of some of the observers to detect the first arrivals, which often do not remain in the area for long, e.g. the account for Blythwood Mission in the Eastern Cape (Godfrey 1928, 1934; Pike 1954).

The two possible sightings in central SWA are not included in this map (compare Figures 2 and 3). Because of the lack of available information it was not possible to plot a 1930 distribution limit for the species in the Transvaal. The lack of published records of first arrivals might indicate that the distribution was stable at this time. The range expansions westwards up the Okavango and Zambezi Rivers might simply be an artefact of inadequate coverage of these areas earlier than 1960.

There is some confusion as to where the two subspecies B. h. hagedash and B. h. erlangeri meet in Mozambique. Roberts (1940) attributes a Beira specimen to B. h. erlangeri but Pinto (1965) attributes Gorongosa birds to B. h. hagedash. Birds from lower down the Urema River are placed in B. h. erlangeri (Clancey 1970). As pointed out by Plowes (1967), there is apparently a large tract south of Gorongosa between the eastern highlands of Zimbabwe and Beira which was, at least until the 1960s, free of hadedas. We have chosen to indicate this area as constituting the break in distribution between the two subspecies.

Using published figures on the areas of the different countries situated south of the Cunene and Zambezi Rivers, i.e. SWA, Botswana, Zimbabwe, Mozambique south of the Zambezi, South Africa (sensu lato), Swaziland and Lesotho, we calculated a total area for this region of 3 407 500 km². The range of the hadeda occupied 530 900 km² (1910), 565 200 km² (1930), 740 700 km² (1955), 934 600 km² (1970) and 1 323 300 km² (1985).

Possible explanations for the expansion in range

The following explanations were investigated.

**Reduction in persecution by man**

It is possible that the recent expansion in the species' range has occurred simply in response to a reduction in man-induced mortality. However, if this were so, then we should search for (a) indications of a wider distribution before the advent of...
modern man in the region, (b) evidence that the species was heavily persecuted by man, and (c) evidence that the level of persecution diminished immediately before or at the same time as the expansion occurred.

There are no published records of hadeda fossils from anywhere in southern Africa. The only distribution records made by early travellers in areas outside their subsequent distribution ranges are Sparrman's record from the George area in 1775 (Skead 1966), Barrow's from the Colesberg area in 1797 [this record is considered doubtful (Skead 1966)], Dobie's from the Umtata area in 1862 (Dobie 1945; Skead 1966) and Wahlberg's from Lake Ngami in the 1850s (Geldenstolpe 1934).

Arbousset & Daumas (1846) and Ayres (1871) recorded the hadeda in the lower Vaal River but its status there was unspecified in the 1830s and it was a rare vagrant in the 1870s. It was not recorded from there again until the 1950s (Brandt 1960; Skead 1970). Smith's rather vague statement, 'pretty frequent in the interior districts' (Roberts 1936), might be taken as an indication that the species was more common in the 1820s and 1830s than was the case in 1906 (Stark & Slater 1906). However there is uncertainty as to which 'interior regions' Smith was referring. The evidence for a range contraction is thus slight, the George and Umtata areas being the only ones where a man-induced range reduction is probably indicated.

That the species was extensively hunted for food by man in the early years of the colonial period emerges from many of the contemporary accounts (e.g. Gurney 1865; Sheppard 1909; Dobie 1945; Turner 1907; Woodward & Woodward 1875).

Towards the end of the nineteenth and the beginning of the twentieth century several authors indicated that the species had declined in abundance in recent years, e.g. Davies (1907) in the Transkei, Gurney (1865) and Ayres (in Layard & Sharpe 1884) writing from Natal and the Woodward brothers reporting on the situation in Zululand (Woodward & Woodward 1899). The regular return of the hadeda to a favoured roosting spot was identified by several authors as the reason they were so easy to shoot (e.g. Shortridge 1904; Woodward & Woodward 1899).

The other southern African ibis which was hunted for food and which roosted colonially, the bald ibis Geronticus eremita, was eliminated from large portions of its original distribution range, with overhunting being one of the suspected causes (Siegfried 1966). In this connection it is possibly significant that the hadeda persisted in the Knysna and Uitenhage areas where the extensive forests would have made the location of roosting sites difficult for hunters. It has been observed that they often roost deep in the forest patches (Skead 1964).

The first nationwide legislation protecting all species of wild birds in South Africa was promulgated in 1934. The hadeda was scheduled a protected bird in the Transvaal in the provincial Ordinance No. 11 of 1935 (Bigalke 1936). In 1941 the species was declared a protected species in Natal (Ossowski 1952), after which major range expansions occurred (Figure 3). Ossowski (1952) observed that the population of hadedas in Natal had increased 'since the introduction of Proclamation No. 6' and obviously considered there to be a causal relationship.

Construction of dams
The creation of artificial water bodies in areas that previously
held no perennial standing water has resulted in numerous aquatic bird species expanding their southern African ranges (McLachlan 1970). The hadeda often nests over water (73% of the 211 nests for which position was recorded in the SAOS nest record collection).

In order to test whether nesting over artificial impoundments has been important in the areas into which the hadeda has extended its distribution, the SAOS nest records from the pre-1910 ('original') and post-1910 ('new') distribution ranges were analysed. About 22% of the 49 nests, for which the position was recorded, were located over dams in the new range. The comparable statistics for the original range were 8% of 149 nests. The chi-squared test showed significant differences in the frequency of occurrence of nests over impoundments versus natural water bodies in the new and original ranges ($\chi^2_{1,DF} = 7.32; p < 0.05$). The same test, comparing the frequency of nests over dams with those over all other known substrata, was also significant ($\chi^2_{1,DF} = 7.44; p < 0.05$). However, there were no significant differences in the frequency of nests over water as against over the ground in the two areas ($\chi^2_{1,DF} = 0.08; p$ N.S.).

If these nest record cards are taken as constituting an unbiased sample (which is unlikely, as dams are often favoured bird-watching localities and nests located here will tend to be preferentially reported) then this artificial habitat is currently providing roughly 12% of the southern African breeding population with nest sites. Artificial impoundments are thus undoubtedly a significant factor in the population's reproductive capacity.

It is also possible that dams have provided a critical feeding habitat for the species in its new range. In the more arid portions of its range the species is known to feed in aquatic habitats, e.g. the Limpopo and Zambezi Valleys (Smithers & Hayes 1958; Cooper 1972; Hamner 1976). The species has been recorded feeding in artificial impoundments, even to the extent of submerging its head entirely during probing (Howe 1984). However, Raseroka (1975) has shown that even in a drier portion of the eastern Cape (the Victoria East district, mean annual rainfall approximately 550 mm/year) the species feeds almost entirely on terrestrial invertebrates.

Our conclusion is that, although artificial impoundments are used more often in the new range than in the original range, this factor has not alone been responsible for the observed expansions.

### Planting and spread of alien trees

Trees are important as both nesting and roosting sites for the hadeda: of the 226 SAOS nest record cards for which the nest site was specified, only two were not in trees (one in a cave and one on a telephone pole (the same as reported by Uys & Broekhuysen 1966)). The importance of tree roost sites for the hadeda has been stressed by numerous observers, e.g. Gurney (1865), Shortridge (1904), Sclater (1912), Bergh (1942), Skead (1951), Ossowski (1952), Nixon (1972) and Winterbottom & Winterbottom (1984). The most recent edition of Roberts' Birds of Southern Africa indicates, for the first time, that the species also uses power pylons as roost sites (Maclean 1985).

In order to test the hypothesis that the planting and spread of alien trees has enabled the hadeda to expand its range in southern Africa, the SAOS nest record cards were analysed for the type of tree utilized for nesting in the original (pre-1910) and new ranges. In the original range, 24% of the 100 nests for which the nest tree was identified were in alien tree species. In the new range, 45% of the 29 nests were in aliens. These frequencies were significantly different ($\chi^2_{1,DF} = 4.77; p < 0.05$). If nests that were placed in 'willow trees' (where the distinction was not made on the nest record card between the alien willow *Salix babylonica* and the various indigenous *Salix* species) were all taken to be in the alien *S. babylonica* [see Macdonald (1986) for the justification for this assumption], then the percentage of nests in alien trees in the original range is 39% ($n = 125$) and that in the new range is 59% ($n = 59$). These frequencies are also significantly different ($\chi^2_{1,DF} = 4.72; p < 0.05$).

Overall, alien trees constitute 29% ($n = 129$) of the nesting trees for which the identity is given on the nest record cards. If the 'willow' tree records are taken as all being from alien willows this increases to 43% ($n = 164$). However, this is likely to be an overestimate of the proportion of nests in alien trees because: (a) 56 nest records came from trees whose identity was not given, though most of these are likely to be indigenous species as observers are generally unable to identify indigenous species while being familiar with most of the common alien species; (b) nests are more likely to be reported from garden situations (where aliens predominate) than from rural situations; (c) rural habitats cover the vast majority of the hadeda's range in southern Africa. The extent of these biases in the nest record card collection is unknown and consequently it is not possible to estimate what contribution nests in alien tree species are currently making to the reproductive output of the region's hadeda populations. Notwithstanding this, we can state with a fair degree of confidence that alien tree species are playing a more important role in the area of recent range expansion than in the species' original range. That the dependence on alien trees is by no means absolute in this new range, indicates that alien trees have not alone been responsible for the range expansion. This contention is borne out by the observation of Collett (1982) that the species uses the indigenous *Acacia karoo* as well as alien *Populus* spp. for nesting and roosting in the recently colonized Cradock district. However, in certain portions of the hadeda's new range, e.g. the fynbos biome, the central Karoo and the grasslands of the Orange Free State and Transvaal, the dependence on alien trees for nest sites appears to be high.

Using the SAOS nest record cards, the following information on the species of alien tree involved can be deduced: Poplars *Populus* spp. seem to be important in the Karoo and grasslands ($n = 7$) with the alien willow *S. babylonica* being so in the fynbos and grassland regions ($n = 6$ definite and 28 possible). Gum trees *Eucalyptus* spp. ($n = 4$), pines *Pinus* spp. ($n = 7$), and black wattle *Acacia mearnsii* ($n = 8$) have been used in the eastern Cape and Natal. *Arbutus* sp. ($n = 1$), *Cupressus* sp. ($n = 3$) and *Grevillea robusta* ($n = 1$) have also been used. Published accounts indicate that wattle plantations can sometimes provide important nesting sites (e.g. Standen 1960).

Alien trees are also important as roosting sites in the new range of the hadeda (e.g. Bergh 1943; Collett 1982; Winterbottom & Winterbottom 1984). In the case of the birds frequenting the Jonkershoek Valley, Stellenbosch it was found that they roosted in the same grove of *Salix babylonica* every night on which they were observed in 1984/1985 (D.M. Richardson, unpubl.)

During the midday heat it has been observed that a single hadeda took shelter in an alien *Populus* grove at Grootsfontein farm near Reivilo, in September 1977 and that a pair behaved similarly just north of the Karoo National Park in January 1985 (I.A.W. Macdonald, unpubl.)

Not only have alien trees provided new nesting and roosting
sites but stands of these trees also provide new feeding sites. In particular the species has been observed to feed extensively in stands of *Acacia mearnsii* in Natal (Clarke 1904; Ossowski 1952).

In order to see whether the species' expansion of range within the Cape is correlated with the progressive afforestation of the province with alien timber trees, the area of its range is plotted together with that of the major plantation species (*Pinus* and *Eucalyptus* spp.) in the Province. There is apparently no direct correlation (Figure 4). Statistics are not available for the increase in the area within 'flying distance' of these plantations — this statistic would probably be more significant for the hadeda which uses these plantations mainly as roosting and nesting sites. Information on the growth in areas affected by the planting and unaided spread of species such as *Populus* spp. and alien *Acacia* spp., which are also used by hadedas, is also not available.

We conclude that, although alien trees have been important in promoting the spread of hadedas into certain areas within its new southern African range, the expansion has not depended totally on these trees. It is only in areas such as the eastern Orange Free State grasslands where, in 1894, on a journey from Bloemfontein to Lesotho, Balfour (1895) could state 'except at one or two farms (where the Boer had planted a poplar or a weeping willow near his "dam"), and along the banks of one river [the Mud River], I do not remember seeing a single tree the whole way', that the provision of trees for nesting and roosting seems to have been essential to the range expansion of the hadeda.

**Increase in extent of irrigation**

In the eastern Cape, Skead (1966) concluded that irrigation alone could not explain the hadeda's range expansion. Subsequently Raseroka's (1975) study from the Victoria East area showed that the species was feeding mainly on invertebrates obtained from the soil surface and not by probing into the soil as had previously been supposed (cf. Ossowski 1952). He concludes that irrigation is thus not essential for the species' range expansion into drier areas. However it is not clear from Raseroka's (1975) data what proportion of the hadeda's food was provided by surface-dwelling invertebrates obtained in irrigated lands. One of the important food items, the larvae of *Spodoptera abyssinica*, which made up 24% by weight of the stomach contents examined, is an insect of irrigated pastures in this area (A.J. Prins, pers. comm.). The hadeda is considered to have moved into the Cradock district in response to the development of irrigation (Collett 1982).

The two separate estimates of 'the area of irrigated farms' and 'areas under irrigation' within the Cape Province are plotted against the year of these estimates in Figure 4. The increase in the range of the hadeda appears to correlate better with irrigation than afforestation. Neither the statistical significance of this correlation nor any indication of a causal relationship in the apparent correlation can be determined.

We conclude that the increase in the area of irrigated lands has probably been a contributory factor in the range expansion of the hadeda.

**Short-term fluctuations in climate**

It is possibly significant that major expansions in range occurred in the late 1950s and the late 1970s, both of which were periods of above-average rainfall for the region (Tyson & Dyer 1978; Tyson 1980). Similarly, the period around the turn of the century, when the range appeared to be reduced relative to some earlier records, was the only period within the historical record when two below-average rainfall decades followed one another (Tyson 1980). It has been stated that the species is subject to mass die-offs during drought periods 'due to their inability to insert their bills into the hard, sun-baked soil' (Ossowski 1952).

However, it is not possible to attribute the recent range expansion totally to these fluctuations in rainfall as the range has expanded progressively since the turn of the century without major retractions during below-average rainfall periods. There has been no progressive increase in regional rainfall over the historical period (Tyson 1980).

**Other possible causes**

The clearance of scrub has been suggested as another possible cause of the observed range expansion (Vernon 1972). We have located only one reference which possibly supports this contention. In the Settlers Park Nature Reserve in Port Elizabeth the frequency of occurrence of hadedas increased by 38% from 1969 to 1972. This increase was attributed to the clearance of scrub and its replacement with lawn in the reserve during the intervening period (Nixon 1972). On a subcontinental scale, however, the indications are that there has been an overall increase in scrub vegetation during the historical period, not a reduction (e.g. Skead 1967; Rowland 1974; Collett 1982). We therefore consider that scrub clearance is unlikely to have been a significant factor at anything but a local scale, in the hadeda's range expansion. In so far as the hadeda commonly nests and roosts in the indigenous *Acacia karoo* in its new range in the eastern Cape (Collett 1982; SAOS nest record cards) and this tree species has increased in abundance over the historic period (Skead 1967; Collett 1982), it is possible that the converse has occurred, i.e. that the range expansion has been promoted by an increase in indigenous woody plants.

A final possibility that needs to be considered relates to the observation that hadedas frequently feed on coprophagous insects in the dung of large mammals (Skead 1951; I.A.W. Macdonald unpubl.). Although published studies on the diet of the hadeda do not show these insects to be the major food item, they are significant (Ossowski 1952; Raseroka 1975) and are possibly more so in times of food shortage (cf. Skead 1951). The recent colonization of the northern Orange Free State grasslands by the glossy ibis *Plegadis falcinellus* has apparently been made possible by their feeding on the dung heaps of intensive livestock production units (B.J. Hain, pers.

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**Figure 4** The area of the hadeda's range in the Cape Province from 1910 to 1976 compared to the areas of some possibly related habitats (all areas expressed as the % of their 1976 values). 1 = area of hadeda's range (1976 = 262 800 km²); 2 = total area under irrigation (1976 = 5 900 km²); 3 = area of irrigated farms (1976 = 11 280 km²); 4 = area afforested with pines and eucalypts (1976 = 887 km²).
comm.). Early in the historic period the indigenous ungulate herds were effectively destroyed over much of the area into which the hadeda has recently expanded its distribution. It is possible that this resulted in the elimination of a food source which was crucial during stress periods. It might not be the provision of irrigated pastures per se that has promoted the subsequent expansion of the hadeda’s range into these areas but the increased availability of the dung of the dairy cows grazing on these pastures. Certainly another spectacular range expansion of this century, that has been linked to an increase in irrigated pastures, has occurred in the cattle egret Bubulcus ibis (Vernon 1972), which is commensal with grazing mammals. However, in the egret it is the increase in irrigated pastures and not changes in cow numbers which has been implicated as the causal factor in the range expansion (Siegfried 1978).

Concluding comment

It is desirable that southern African ornithologists develop systems for detecting changes in distribution so that they are accurately and rapidly recorded. All the uncertainties of retrospective historical ecology, so prevalent in the present study, will be replaced where these changes can be observed and immediately investigated in the field. We hope that the imminent creation of a southern African Bird Population Data Bank (Ledger 1985) will go a long way towards filling this need.

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