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The breeding status and colony dynamics of Cape Vulture *Gyps coprotheres* in Botswana

WENDY D. BORELLO and REMIGIO M. BORELLO

Summary

Cape Vulture *Gyps coprotheres* is endemic to southern Africa and is globally threatened. Colonies in Botswana comprise part of one of the two core breeding areas in the species's range, and very little has previously been published about them. Ground censusing of 11 Cape Vulture sites in Botswana was undertaken from 1992 to 1999, continuing a monitoring programme initiated by the authors in 1984. Survey methods and census procedures are documented. The potential Cape Vulture breeding population in Botswana is estimated to be about 600 pairs, comprising at least 100 pairs at Mannyelanong in the south-east and about 500 pairs in eastern Botswana. This represents an increase from previous estimates, and reflects improved census techniques rather than an increase in population size. The mean turnover rate of nest site usage from one year to the next averaged 21% at Mannyelanong, and was about 26% at Manong Yeng in eastern Botswana. Annual productivity of nest sites increased with the number of years the site had been occupied. Over the eight years of study eggs were laid in at least 436 of 477 nests (91.4%) at Mannyelanong; chicks survived to mid season (60–80 days old) in 327 nests (75% of eggs laid), and fledged (best estimate) in 248 nests (56.9% of eggs laid and 52% of pairs attempting to breed). In eastern Botswana eggs were laid in at least 1,825 of 2,101 nests (86.9%); chicks survived to mid season in 1,272 nests (69.7% of eggs laid). Two seasons have been excluded for eastern Botswana (1994 and 1995) due to incomplete data, and breeding success can be estimated only from 1997 to 1999: of 990 eggs laid out of 1,108 nests, chicks fledged in 384 nests (38.8% of eggs laid and 34.6% of pairs attempting to breed). The eastern Botswana breeding population remains in a state of flux following the collapse of a primary colony that was the country's Cape Vulture stronghold. Conservation concerns and the vulnerability of Cape Vulture sites are discussed.

Introduction

Cape Vulture *Gyps coprotheres* is listed by the ICBP/IUCN as a 'Vulnerable' globally threatened species (Collar *et al*. 1994). It is a gregarious, cliff-nesting species occupying breeding colonies year-round, and is endemic to southern Africa. In Botswana the Cape Vulture's breeding and roosting sites are restricted to the eastern hardveld, with two discrete populations located in the south-east (25°03'S, 25°45'E) and east (22°40'S, 27°30'E) (Figure 1). From 1984 onward we have been monitoring the population and breeding performance at all Botswana's colonies, and have also located and documented several previously unknown sites (e.g. Borello and Borello 1987a). Descriptions of the Botswana colonies, data on status and demographic trends from 1984 until mid 1992, and conservation aspects are documented in Borello (1985, 1987) and Borello and

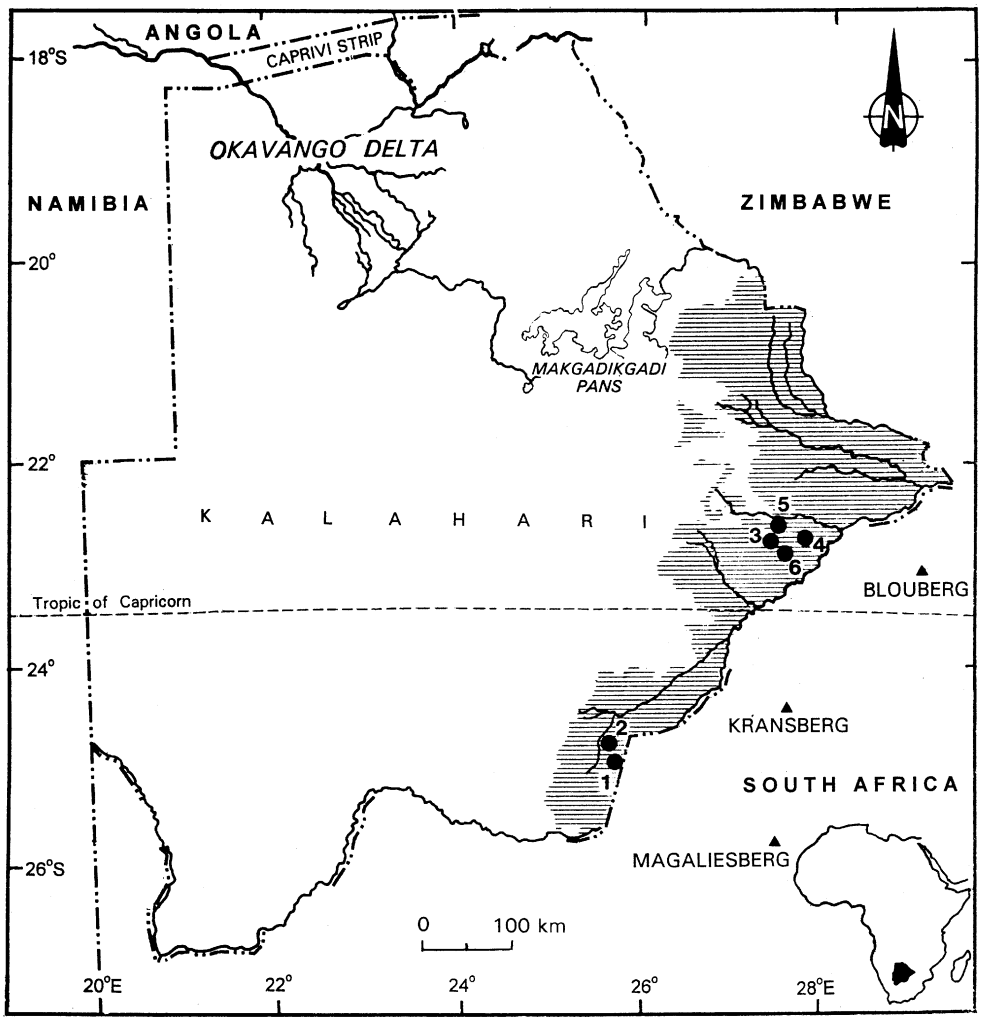

Figure 1. Map of Botswana showing the eastern hardveld (shaded), the main Cape Vulture sites (filled circles) of the south-eastern (1, Mannyelanong; 2, Manyana) and eastern (3, Manong Yeng; 4, Kukubye; 5, Bonwalenong; 6, Makoote-Sefhare) populations, and the proximity of neighbouring Cape Vulture populations (triangles) in South Africa. The geographical coordinates of all the Cape Vulture sites are listed in Table 1.

Borello (1987b, 1992, 1993 and references therein, 1997a). The basic framework of the Cape Vulture monitoring programme that we established in 1984 remained unchanged, although maintaining our long-term data-set enabled changes within the colonies to be detected more efficiently.

This paper provides updated estimates of population numbers and reproductive success. It also outlines grave concerns regarding human disturbance at the Cape Vulture colony at Mannyelanong in south-east Botswana, and some related concerns regarding the important breeding sites in the Tswapong Hills (eastern

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Table 1. Location and status in 1999 of Cape Vulture *Gyps coprotheres* sites in Botswana

Site name	Region of Botswana	Geographical coordinates	Status (1999)
Mannyelanong	South-eastern	25°03′30″S 25°45′30″E	Breeding
Manyana	South-eastern	24°50′30″S 25°39′00″E	Occasional roost
Otse	South-eastern	25°01′15″S 25°44′00″E	Abandoned
Baratani	South-eastern	25°00′07″S 25°44′22″E	Abandoned
Manong Yeng	Eastern (Tswapong complex)	22°40′00″S 27°25′00″E	Breeding
Kukubye	Eastern (Tswapong complex)	22°44′55″S 27°44′55″E	Breeding
Machibaba	Eastern (Tswapong complex)	22°45′59″S 27°44′59″E	Breeding
Bonwalenong	Eastern (Tswapong complex)	22°37′00″S 27°26′00″E	Breeding
Seolwane	Eastern (Tswapong complex)	22°39′33″S 27°40′48″E	Abandoned
Sebale	Eastern (Tswapong complex)	22°37′30″S 27°37′10″E	Roost/breeding
Makoote-Sefhare	Eastern	22°59′41″S 27°29′50″E	Roost/breeding

Botswana) since the collapse in 1995–96 of the largest breeding colony in this country.

Materials and methods

Eleven Cape Vulture colonies in Botswana were studied (Table 1). Data were collected during the breeding season (May to December) by monthly ground surveys in south-eastern Botswana (Mannyelanong and Manyana), and mainly biannual surveys in eastern Botswana (Bonwalenong, Kukubye, Machibaba, Manong Yeng, Sebale, Seolwane, and Makoote-Sefhare). Some additional visits were made during and outside the breeding season. Cape Vultures usually lay a single egg, average incubation is 57 days, and the nestling period to fledging averages about 143 days (Robertson 1986). Observations were made with a 3.5-inch Duplex Questar 81–130× telescope, a Kowa 20–60× spotting scope, Zeiss 10 × 40 binoculars, and a tape recorder. With the exception of Mannyelanong where it was possible to drive to the base of the scree slope, all the Cape Vulture breeding and roosting sites were accessible only on foot. Descriptions of observation points and techniques are given in Borello and Borello (1993).

Assignment of nest site numbers

At Mannyelanong, Kukubye and Manong Yeng all known nest sites were plotted onto enlarged or close-up photographs of the colony cliff faces and each assigned a permanent number. Roosting or loafing places, even if regularly used, were not assigned a number unless a pair had bred there, although all such places with pairs present were noted and plotted at each visit.

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Census procedure

We attempted to make counts at standardized times during the breeding season. Very early morning (before sunrise) or late afternoon counts gave the highest numbers of roosting birds, including partners at nests. One adult was normally in constant attendance at an active nest, even when young were almost fully grown. Breeding partners, when present at the colony, generally roosted next to the nest site, including those that had failed in their breeding attempt, and most non-breeders occupied well-used ledges (identified by nest site number or white mutes covering the rock). Nevertheless movement within the colony began early in the morning before the birds left to forage. Many moved to sunning spots or onto communal roosting areas on the rock faces, and it was therefore important that counts were made before this occurred. At least two counts were made in quick succession. The plotting of nest-sites and re-recording their status onto data sheets was incorporated into the second count.

We tried to age all birds present according to plumage features (see Piper *et al*. 1989, Mundy *et al*. 1992). Although our counts of juveniles, first years, second years and older immatures were more reliable, recruitment of younger birds (first breeders) could not be easily established. A known-age Cape Vulture into its fourth year had the characteristic adult plumage, with the exception of eye colour (W.D. Borello and R.M. Borello unpubl. data). We found that birds of that age class were mostly indistinguishable from adults, despite variation between individuals, because eye colour at observation distances was not easily discernible. Consequently, mixed age or inexperienced subadult pairs were practically undetectable, contrary to previous descriptions of subadult characteristics (e.g. Piper *et al*. 1989).

Calculations of breeding success rates should be based on the total number of pairs at the colony i.e. including non-breeding pairs occupying nest sites. Inevitably, however, non-breeding birds may be undercounted because many will be absent on any one counting day. Counts were therefore structured to allow a breakdown into the following components:

1. Active nests, further categorized as
   i. adult present on a nest in an incubating or brooding position, or adult in attendance at nest with nestling
   ii. a nestling or juvenile on a nest but with no adult present
2. Number of birds present at an active nest (i.e. both partners)
3. Single bird or pair at an empty or failed nest
4. Roosting or loafing pairs, i.e. no nest, and whether at a numbered nest site, or not
5. A single bird tenanting a numbered nest site

The location of tenanted nest sites and pairs roosting were plotted at each visit onto a separate transparent acetate sheet overlaying enlarged photographs of the cliff face in order to compile a history of the movements and occupied ledges for each visit each season. The number of breeding individuals was subtracted from the total number of adults present at each census to give an estimate of the non-breeding population.

Breeding terminology

Monitoring was conducted as unobtrusively as possible to avoid disturbance. As a consequence, with the exception of Bonwalenong, it was impossible to establish the exact contents of each nest at all times. Pairs ''attempting to breed'' were those building a nest; ''breeding'' occurred when an egg was laid. Since the egg could rarely be seen, it was assumed that laying had occurred when an adult was lying flat on the nest in typical incubating position. The later presence of a nestling confirmed egg-laying. An ''active nest'' was one containing an egg or a nestling. Because monitoring took place at intervals, a laying attempt may have been overlooked if, for example, an adult was not on its nest at the first census (when the nest would be described as ''empty''), and was then again absent at subsequent counts because an egg had been stolen or rolled out of the nest. ''Mid season productivity'' referred to 60 to 80-day-old nestlings. The ''breeding success rate'' was based on the number of probable breeding attempts (i.e. pairs laying an egg) and the number of young reaching the fledging stage. Nest sites described as ''occupied'' or ''used'' signified construction of a nest, i.e. attempted breeding, at that site. ''Tenanted'' nest sites were those with pairs or individuals present, but not necessarily breeding birds, during any census. Nest sites described as ''abandoned'' were those that were in use at the beginning of the study period, but appeared to be totally deserted for breeding, roosting or loafing, by 1999. They were characterized by a complete lack of ''whitewash'' at the site and surrounding area and, in some cases, the growth of vegetation. As unused sites could be the result of ''gaps'' in usage, i.e. continued tenancy, or periods of ''non-tenancy'' (no birds seen roosting or loafing during a census), with the site re-occupied thereafter, ''abandoned'' nest sites have been identified with caution.

Results: south-eastern Botswana

Population counts

Over the eight years 1992–99 the number of pairs attempting to breed annually at Mannyelanong plus the highest estimated number of non-breeding birds present during a census gave a mean population estimate of 104 pairs (S.D. = 8.8, range 93–122). The estimated maximum number of pairs present for each year varied from 94 to 123 (Table 2).

Since our monitoring programme began in 1984, we have seen rather few immature birds at the colony (e.g. Borello and Borello 1992). From June 1992 to July 1999 numbers varied from nil to 21 (n = 54 counts, mean 6.4, S.D. = 4.88), and many of these (201) were first-year individuals. Fewer (142) older immatures were recorded and most were second-year birds. Cape Vulture, a long-lived species, has more than one immature plumage and generally acquires definitive adult dress when six or seven years old (Piper *et al*. 1989).

Nest site occupancy and turnover

A total of 142 separate nest sites were identified. Not allowing for re-use of previously known traditional sites prior to 1992 – the year when a unique code

Table 2. Maximum counts for each season (1992-1999) of the potential breeding population of Cape Vultures at Mannyelanong, south-eastern Botswana. The possible number of pairs is the actual number of pairs attempting to breed plus the number of non-breeding individuals (excluding immature birds) divided by two into pairs (half-pairs were rounded upwards)

Date	Total adults present	Non-breeding adults present	Total no. of pairs attempting to breed	Possible no. of pairs at colony
23/09/92	138	89	64	109
23/09/93	182	117	64	123
09/08/94	149	61	65	96
10/12/95	142	103	49	101
26/08/96	156	99	59	109
23/09/97	134	79	63	103
23/09/98	109	77	55	94
25/08/99	154	80	58	98
Mean (± S.D.)				104 (± 8.8)

and number was assigned to each site where breeding was attempted – 60 additional nest sites were established during the study period (Table 3), an average of 8.6 new nest sites initiated per year. If calculated according to Robertson's (1984) criterion for nest site usage (i.e. attempted breeding or breeding in consecutive years) to enable direct comparison, re-usage of sites at Mannyelanong over seven cycles (1992 cf. 1993, 1993 cf. 1994, etc.) averaged 42% (range 30–53) (Table 4). Nest site fidelity could not be reliably established because most of the vultures

Table 3. Number of new nest sites and productivity of Cape Vultures each breeding season at Mannyelanong, south-eastern Botswana from 1992 to 1999

	1992	1993	1994	1995	1996	1997	1998	1999	Success rate
No. of nest sites	82	82	90	96	106	116	132	142	
New nest sites		0	8	6	10	10	16	10	
Breeding at new site			5	6	8	10	10	9	
Young raised to fledging at new site			5	2	3	5	2	5	0.46 0.37

Table 4. Usage of nest sites by Cape Vultures at the Mannyelanong colony where attempted breeding or breeding occurred in consecutive years over seven cycles from 1992 to 1999

	No. nests used previous year	No. nests re-used	Percentage re-used
1992–93	82	46	56
1993–94	82	53	65
1994–95	90	37	41
1995–96	96	34	35
1996–97	106	46	43
1997–98	116	30	26
1998–99	132	33	25
Total/mean	698	279	42

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Table 5. Turnover in nest site usage (i.e. attempted breeding) at the Mannyelanong Cape Vulture colony from 1992 to 1999

Period	Used in year 1 but not year 2 (total no. of sites in year 1 in brackets)	Used in year 2 but not year 1 (total no. of sites in year 2 in brackets)	Turnover rate[a]
1992–93	10 (64)	6 (64)	0.13
1993–94	5 (64)	9 (65)	0.11
1994–95	18 (65)	7 (49)	0.22
1995–96	10 (49)	15 (59)	0.23
1996–97	7 (59)	14 (63)	0.17
1997–98	26 (63)	17 (55)	0.36
1998–99	14 (55)	18 (58)	0.28
Mean nest site turnover rate 1992 to 1999			21%

[a] (No. sites used in year 1 but not in year 2 + total no. sites used in year 2 but not in year 1) divided by (total no. sites used in year 1 + total no. sites used in year 2). Nest sites with gaps in usage, indicating possible breeding periodicity or erratic periods of tenancy, have been excluded from the calculations.

were not individually identifiable. In two instances a recognizable individual bred at the same site for two consecutive years.

The spatial distribution and density of nests changed during the study period and this was reflected in the turnover rate of occupied nest sites, which varied annually from 10% to 36% (mean 21%), suggesting a high level of movement (Table 5). Isolated nest sites were not necessarily less frequently used. Nest sites with gaps in usage were excluded from the turnover calculations. Gaps in nest site usage could occur for 1–5 years but did not necessarily mean gaps in ''tenancy'' (an individual or pair standing, loafing or roosting at a known nest site). A gap in nest usage occurred significantly more often in years following a failed breeding attempt (mean 49% unoccupied, range 29–100%) than in years following a successful breeding attempt (mean 22% unoccupied, range 0–42%; $\chi^2 = 27.4$, d.f. = 1, $P < 0.001$; Table 6).

Eight sites that had been occupied for between three and eight consecutive years were not abandoned despite two or three successive reproductive failures at each. We do not know whether these sites were occupied by long-term pairs with strong site fidelity, or inexperienced pairs attempting to establish themselves, or whether failed pairs were simply replaced immediately by new pairs. Conversely, some entire ledges or areas of cliff face were abandoned during the course of the study despite successful breeding there previously. These birds

Table 6. Nest site reoccupancy in relation to reproductive performance of Cape Vultures at the Mannyelanong colony between 1992 and 1999

	No. sites reoccupied in year 2	No. sites unoccupied in year 2	Totals
No. nest sites successful in year 1	166	46	212
No. nest sites failed in year 1	99	94	193
Totals	265	140	405

χ^2 analysis involved $n = 405$ comparisons among 132 different nest sites over 8 years.

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Table 7. Breeding performance of Cape Vultures in south-eastern Botswana (Mannyelanong) from 1992 to 1999

	1992	1993	1994	1995	1996	1997	1998	1999	Totals	%
Pairs attempting to breed	64	64	65	49	59	63	55	58	477	
Breeding	62	59	57	48	53	62	40	55	436	91.4%
Mid season nestlings (survivors to 60–80 days old)	43	51	48	44	36	43	17	45	327	75%
Successful (young reaching fledging stage)	27	40	43	31	35	26	10	36	248	56.9%[a] 52%[b]

[a] Of eggs laid
[b] Of pairs attempting to breed.

may have emigrated from the colony but local shifts to other parts of the cliff face could not be ruled out.

Breeding success

Of an estimated total potential breeding population of 104 pairs, an average of 49 pairs (47.6%; range 41–63) per season over eight years did not breed (i.e. lay an egg). The average final productivity (young brought to fledging stage) per season was 30.2%. Over the eight years of study, eggs were laid in at least 436 out of 477 nests (91.4%), chicks survived to mid season (60–80 days old) in 327 nests (75% of eggs laid), and fledged (best estimate) in 248 nests (56.9% of eggs laid and 52% of pairs attempting to breed). The success rate of probable breeding pairs (measured as eggs producing fledglings) in 1998, the lowest during the present study, was only 25% (10 nestlings fledged) (Table 7). Mean annual chick productivity at a nest site increased with the number of consecutive years over which breeding was attempted at the site (Figure 2).

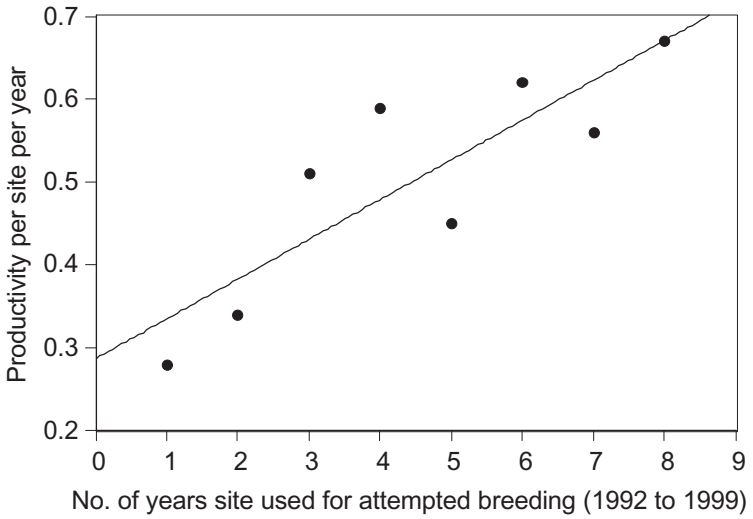

Figure 2. Relationship between productivity and frequency of nest site usage by Cape Vultures at the Mannyelanong colony ($y = 0.287 + 0.048x$, $n = 8$; $R^2 = 73\%$, $P = 0.007$).

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During 1992–99 laying took place mostly over a four-week period from May to June (Figure 3). The estimated median laying dates all fell in June with the exception of 1994 and 1996 when the median dates were in May (Figure 3). We found no evidence to support the suggestion that pairs breeding in close proximity showed synchrony in egg-laying (Mundy 1982, Vernon *et al*. 1984).

Results: eastern Botswana

Prior to 1996 the entire breeding population of Cape Vultures in eastern Botswana was located in the Tswapong Hills. The biggest of these was the Bonwalenong colony in the Moremi Gorge (once known as Eagle Kloof; Willoughby 1900), which held the highest number of potential breeding pairs (an estimated minimum of 250–300) in the country. It was apparently stable and showed no sign of substantial change until 1995–96, when it was completely abandoned. The birds apparently moved to other sites in the region, where numbers increased (see below).

Population Densities

Eastern Botswana has an estimated minimum of 500 potential breeding pairs (calculated by the same procedures as for the Mannyelanong colony), with most of this population located in the Tswapong Hills.

Breeding success

As at Mannyelanong, pairs did not necessarily breed in consecutive years. Of the estimated potential breeding population of 500 pairs an average of 196 pairs (39.2%) over six years (range 65–251 pairs) did not breed in each season. Excluding 1994 and 1995, for which no data were available, eggs were laid in at least 1,825 of 2,101 nests (86.9%); chicks survived to mid season (60–80 days old) in 1,272 nests (69.7% of eggs laid; Table 8). Estimates of fledging success, however, were available only for 1997 to 1999, when the mean value was 38.8% of eggs laid (Table 8).

The overall timing of laying at two colonies for which data were available (Kukubye and Manong Yeng in 1997–99) was the same as south-eastern Botswana. The median egg-laying dates available for these more northerly Botswana colonies ranged from 30 May to 2 June (Table 9).

The colony at Kukubye dwindled from about 70 breeding pairs in 1984 to complete abandonment in 1990 and 1991. Nine pairs then bred at Kukubye in 1992, increasing to 33 in 1993. In 1995 the colony was in a state of flux; 246 adults (and four immature birds) were present, and 53 pairs bred. No birds nested or roosted at Bonwalenong and it was evident that most of that colony's displaced birds had resettled at Kukubye. In 1996 breeding attempts increased: eggs were laid in at least 151 of 176 nests (85.8%) and nestlings survived to mid season in 129 nests (85.4% of eggs laid). Data for breeding success were incomplete. In 1997 a huge breeding effort took place with 296 pairs building nests and at least 279 (94.3%) pairs laying. Chicks survived to mid season in 108 nests (38.7% of eggs laid) but, of these, only 60 survived to the fledging stage (21.5% of eggs laid and 20.3% of pairs attempting to breed). In 1998 eggs were laid in 110 out of 136

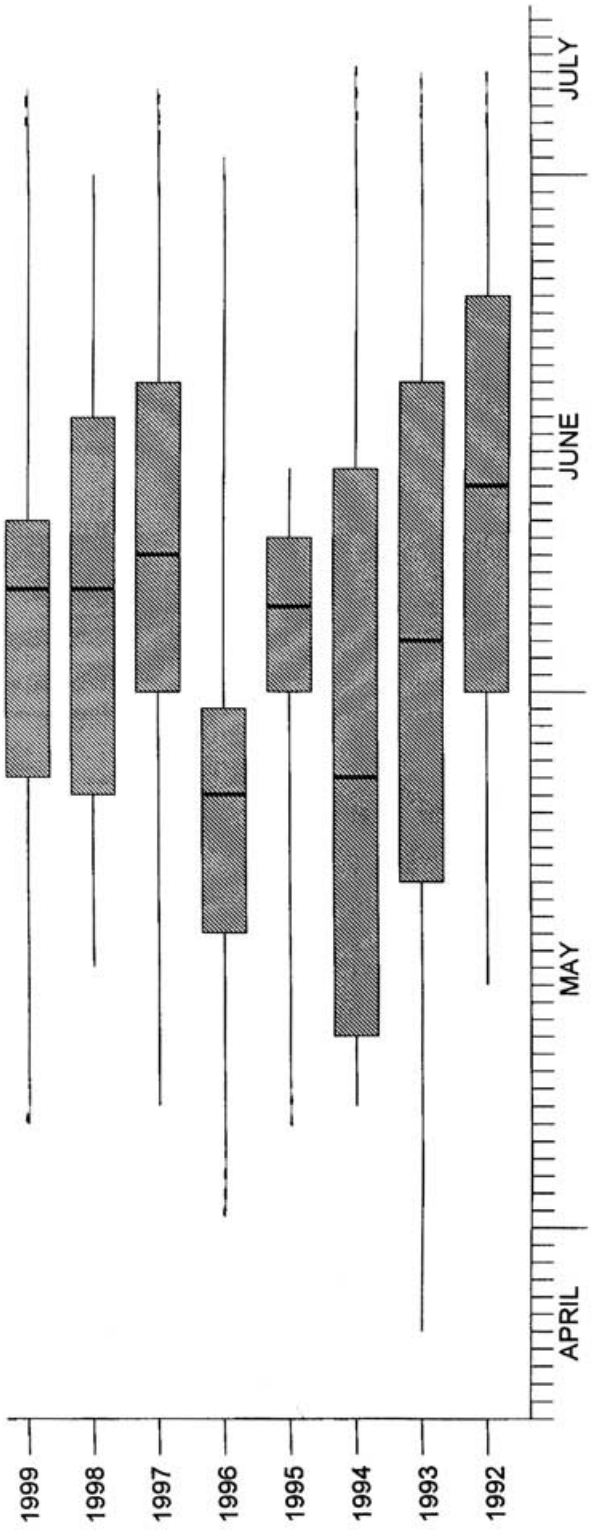

Figure 3. Timing of laying by Cape Vultures at Mannyelanong from 1992 to 1999. Median dates are indicated by vertical lines, shaded bars show the interquartile interval between 1st and 3rd quartile dates, and the overall laying period indicated by horizontal lines. Number of clutches and laying dates were grouped into fortnightly/monthly periods for each year.

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Table 8. Breeding performance of Cape Vultures in eastern Botswana from 1992 to 1999. Incomplete or no data are indicated by dashes. Percentage successful based on 1997–99 only

	1992	1993	1994	1995	1996	1997	1998	1999	Totals	%
Pairs attempting to breed	332	325	-	-	336	472	361	275	2101	
Breeding	285	259	-	-	291	435	306	249	1825	86.9%
Mid season nestlings (survivors to 60–80 days old)	265	224	-	-	212	186	192	193	1272	69.7%
Successful (young reaching fledging stage)	-	-	-	82	-	130	120	134	-	38.8%

Table 9. Breeding seasonality of Cape Vultures from 1997 to 1999 in eastern Botswana at Kukubye and Manong Yeng, showing estimated egg-laying dates, estimated number of eggs laid and median laying dates

	1997	1998	1999
Kukubye			
1–14 May	0	20	0
15 May–14 June	224	73	17
15–30 June	55	17	0
Median date	2 June	30 May	30 May
Manong Yeng			
1–14 May	14	25	28
15 May–14 June	74	83	
15–30 June	21	24	118[a]
Median date	1 June	30 May	2 June

[a] Eggs laid between 15 May and 30 June.

nests (80.9%), chicks survived to mid season in 50 nests (45.4% of known eggs laid) and 21 of those survived to pre-fledging stage (19% of eggs laid and 15.4% of pairs attempting to breed).

During these years there was some further displacement into other Tswapong sites (e.g. an estimated 34 pairs moved to Manong Yeng in 1996, and more pairs in 1998), so that by 1999 most of the vultures that resettled in Kukubye had abandoned it and only 20 pairs attempted to breed there that year. Of these, 17 laid an egg and seven nestlings survived to mid season but only one was present at the final census (although it is likely that at least two had fledged successfully). The mean breeding success rate in 1997, 1998 and 1999 was therefore only 13.4% (S.D. = 5.3).

The most complete data for the period under review are from Manong Yeng (Table 8), although some seasonal data sets are incomplete (i.e. either egg laying or final productivity cannot be reliably established). The turnover rate of nest sites used from 1992 to 1993, and 1996 to 1999 ranged from 10% to 36% (mean 21%; Table 10). This was not significantly greater than at Mannyelanong (Mann–Whitney $U = 35.5$, $P = 0.25$).

Because there was immigration to Manong Yeng by displaced birds originating in Bonwalenong, we have not based breeding success at this colony on total population size, but on the number of breeding pairs only. Excluding 1994 and

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Table 10. Turnover in nest site usage by Cape Vultures at Manong Yeng from 1992 to 1999. Incomplete or no data are indicated by dashes

Period	Used in year 1 but not year 2 (total no. of sites in year 1 in brackets)	Used in year 2 but not year 1 (total no. of sites in year 2 in brackets)	Turnover rate[a]
1992–93	24 (94)	23 (105)	0.24
1993–94	-	-	-
1994–95	-	-	-
1995–96	-	-	-
1996–97	18 (93)	36 (117)	0.26
1997–98	26 (117)	39 (150)	0.24
1998–99	31 (150)	55 (158)	0.28
Mean nest site turnover rate 1992 to 1993, 1996 to 1999			26%

[a] (No. sites used in year 1 but not in year 2 + total no. sites used in year 2 but not in year 1) divided by (total no. sites used in year 1+ total no. sites used in year 2). Nest sites with gaps in usage, indicating possible breeding periodicity or erratic periods of tenancy, have been excluded from the calculations.

1995, eggs were laid in at least 668 of 717 nests (93.2%) overall; chicks survived to mid season in 457 nests (68.4% of eggs laid). Final productivity can be reliably estimated from 1997–99 only: the mean success rate was 39.8% of eggs laid.

Vultures had previously used the roost site at Makoote-Sefhare only occasionally (Borello and Borello 1992, Brewster 1995), and no birds or evidence of roosting were found there during 1995. Breeding began in 1996 when, of a possible 50 pairs occupying the cliff face, 27 built nests and 23 of those pairs bred (Borello and Borello 1997b). Fewer birds used the site in 1997: of 23 pairs nest building 17 laid eggs (73.9%). There was no evidence of non-breeding pairs roosting there. Seven nestlings survived to fledging (41.2% of eggs laid and 30.4% of pairs attempting to breed). In 1999, following the emigration of birds from Kukubye, a maximum of 151 adults were counted at Makoote, with 58 of those present at active nests, together with 16 non-breeding pairs. In 1999 breeding numbers increased: eggs were laid in at least 73 of 76 nests (96%), 64 nestlings survived to mid season (87.7% of eggs laid) and 63 nestlings survived to fledgling stage (86.3% of eggs laid and 82.9% of pairs attempting to breed).

Colony switching

Switching colonies by breeding adults has been suspected in South Africa at Magaliesberg (Verdoorn and Becker 1992) and among primary and secondary colonies in the Western Cape, where small increases in one place have been matched by decreases at others nearby (Boshoff and Scott 1990, Scott 1997). It has also been evident that some birds in the Tswapong Hills, where the entire eastern Botswana breeding population was located, have sometimes changed breeding sites on a small scale (Borello and Borello 1993). However, as noted above, a substantial change occurred in 1995–96 with the complete abandonment of the Bonwalenong and the resettlement of the birds at other sites in eastern Botswana.

Although the displaced Bonwalenong birds could be accounted for during the years immediately after the colony's abandonment, in 1999 at least 100 pairs could not be located. There was no evidence that these roosted at any other known eastern Botswana site, nor any evidence that the birds moved *c.* 320 km south to Mannyelanong. In July 1999 there were almost no freshly whitened ledges on the cliff face at Kukubye, and only 20 pairs were observed at nests, with no non-breeding birds roosting there. At this time there was an influx of breeding pairs to Makoote-Sefhare, a roosting site on a range of small hills just south of Tswapong that had been used for breeding in 1996 following the abandonment of Bonwalenong (Borello and Borello 1997b); others appeared at Manong Yeng (Table 1). In 1999 about 25 vultures were found once more at Bonwalenong: 10 pairs had built nests and four of these were active. Other individuals moved to Tswapong-Sebale, a small, long-abandoned breeding site that was re-used in 1999 when two pairs bred (eight pairs built nests) and about 20 birds intermittently roosted there.

Apart from the small-scale redistribution of birds within Botswana, we were unable to find any other communal roost sites in the Tswapong Hills despite extensive ground and aerial searches. It remains possible that, for the 1999 season at least, the remaining birds left the Tswapong Hills and moved farther away, the closest other suitable roosting or breeding habitat being the Blouberg Cape Vulture colony in South Africa (23°02′S, 29°03′E), about 164 km to the east. There is firm evidence of adult foraging movements over a similar distance: in 1996 we observed a wing-tagged (#030) vulture copulating (thereby establishing it as a male) and subsequently breeding successfully at a traditional Mannyelanong nest site. As an adult it had been caught and marked in September 1994 while feeding at Thabazimbi (South Africa) *c.* 170 km to the north-east (Borello and Borello 1997a, P. C. Benson *in litt*. 1997). Thabazimbi is only 20 km from a Cape Vulture colony at Kransberg (24°28′S, 27°36′E), where another uniquely marked individual ringed at Mannyelanong has also been sighted (Piper 1994). Temporary or permanent long-range emigration from eastern Botswana therefore cannot be ruled out.

We are not aware of any previous records for Cape Vultures (or any colonial cliff-nesting vulture species) of an entire, large population of breeding and non-breeding pairs plus floaters abandoning a traditional site and relocating elsewhere with such rapidity. One previous large-scale movement was recorded in south-east Botswana (Mundy 1983): by 1973 many birds had moved from Mannyelanong to ''new'' secondary sites (though historical records suggest that these sites may have been used in the past), in particular to a new site, named Manyana (Table 1), near Mogonye. However Mannyelanong (considered the primary site) was not completely abandoned and it seemed instead that a gradual emigration of breeding pairs (49) from Mannyelanong occurred over four years. Seven pairs were still breeding at Mannyelanong in 1973, at least 38 breeding pairs returned in 1974 and in 1975 the population again increased, with the Manyana colony waning. The reason suggested for the initial relocation is that it was probably caused by human disturbance (Mundy 1983). It is unlikely in our view that the sudden abandonment of the Bonwalenong colony can be ascribed to normal Cape Vulture behaviour; rather we should suspect human disturbance there too.

Discussion

Laying dates, breeding performance and nest tenure

The Cape Vulture breeding season in Botswana begins in May, though there is some annual variation in the timing of laying between colonies and years. Piper (1994) stated that the breeding season begins on about 10 April in the northern colonies in South Africa, beginning later farther south. The situation is not as clear-cut, however, not least because the northern colonies in South Africa lie at almost the same latitude (23°S) as the Tswapong Hills, where breeding begins a month later. Almost all Cape Vulture colonies lie within the region of summer rainfall in southern Africa with the exception of Potberg and the Little Karoo colonies in the western Cape Province of South Africa, which lie in the transition zone with the winter rainfall area. Our results partly support the assessment of Mundy *et al*. (1992) that most eggs are laid in May in summer rainfall colonies regardless of their latitude.

Over the study period a lower percentage of Cape Vultures nest-building in eastern Botswana laid eggs (86.9%) than in the south-east at Mannyelanong (91.4%) and the observed mean productivity against eggs laid (38.8%) was also lower than at Mannyelanong (56.9%). It is evident that reproductive success varies within and between years, but the reasons why success may be very low at particular colonies are unknown.

Robertson (1984) showed that at Potberg, South Africa, a pair of Cape Vultures bred at the same nest site over two consecutive years. Although the majority of birds in Cape Vulture colonies, including Potberg, could not be individually recognized, it has been subsequently assumed that once pairs adopt a particular colony (not necessarily the natal colony), site occupancy for two successive years or more indicates long-term nest site fidelity (Mundy *et al*. 1992, Piper 1994). Some pairs may not breed every year: Piper (1994) estimated that about 85% of pairs bred in a given year, i.e. missing about one year in seven. Without individually marked birds, however, it is not known whether gaps in site occupancy indicate missed breeding that year or breeding at another site, and whether tenants subsequently return or are replaced. At Magaliesberg, Potberg and Collywobbles about 80% of sites were reoccupied the following year (Vernon *et al*. 1984, Mundy *et al*. 1992, Piper 1994). At Potberg, Robertson (1984) found that 67% of sites were re-used from one year to the next (range 45–83% over seven cycles). By comparison, at Mannyelanong only 42% of nest sites (range 25–65% over seven cycles) were reoccupied. The mean increment of new nests per year over eight years also differed between Potberg (1.6, Robertson 1984) and Mannyelanong (8.6).

There are evidently many more nest sites at Mannyelanong than are occupied each year by the present breeding population. Despite evidence of nest site fidelity, though this is based on patterns of long-term occupancy rather than recognizable individuals, the turnover rates of nest sites in use from one season to the next at both Mannyelanong (21%; Table 5) and Manong Yeng (26%; Table 10) are high. The annual turnover rate that can be calculated for the Cape Vulture colony at Collywobbles in South Africa from 1980 to 1989 (table 16 in Vernon and Piper 1991) was 12% (range 9–20%), significantly lower than both Mannyelanong (Mann–Whitney $U = 54.0$, $P = 0.019$) and Manong Yeng ($U = 45.0$, $P = 0.006$).

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The difference between the Botswana colonies and Collywobbles is conservative because the Collywobbles data probably included gap birds that would have inflated the turnover estimates, so the real difference is probably even greater.

Whether Mannyelanong and Manong Yeng have higher rates of emigration and immigration than at Collywobbles, or whether established pairs are more prone to change breeding ledges between years, or skip breeding seasons more frequently, remains unknown without marked birds. There was no evidence that less frequently used nests were occupied or new nests initiated only when there was a high number of vultures attempting to breed. The differences in dynamics between the Botswana colonies and Collywobbles do not necessarily reflect differences in their long-term stability. Despite its apparently greater constancy in nest site usage, Collywobbles declined from over 300 pairs in the 1980s to 60 pairs in 1999, attributed to emigration or mortality (Vernon 1999), whereas Mannyelanong and Manong Yeng have maintained overall numbers despite a greater nest site turnover.

Increased length of nest site tenure resulted in markedly higher breeding success, with productivity at nest sites used throughout the eight years of the study being double that at nest sites used only once or twice (Figure 2). A more limited data-set in Vernon *et al*. (1984) suggests a similar relationship between breeding success and nest site tenure among Cape Vultures breeding at Collywobbles. We cannot be sure, however, whether there are simply ''good sites'' where any bird could breed successfully, or whether there are ''good birds'' that happen to reoccupy a site over a number of years. It is possible that seldom-used sites are suboptimal even for experienced adult pairs, or they are generally used only by young birds before better nest sites become available elsewhere in the colony. Fernandez *et al*. (1998) found that subadult Griffon Vultures *Gyps fulvus* breeding in Spain had lower productivity even in good sites. However, because we could not reliably identify subadult or mixed-age pairs in Cape Vulture (see Methods), we cannot distinguish between these possibilities.

Despite the evident advantage of long-term nest site tenure in terms of increased reproductive success, Cape Vulture colonies in Botswana appear to be more dynamic than previously thought. There is a high annual turnover of nest sites within a colony and apparently large-scale switching of breeding birds between colonies in some years but the reasons for this remain unknown. It is puzzling that apparently optimal sites may be abandoned, whereas sites with high breeding failure continue to be occupied. The extent of natal dispersal also requires further study, especially from colonies such as Mannyelanong, for example, which is below its carrying capacity. Boshoff *et al*. (1997) have already highlighted the need for adult birds to be individually recognizable in order to advance Cape Vulture research. Without a high proportion of identifiable adults within a colony, detailed studies of site fidelity and breeding success will not be possible.

Current status and conservation of Cape Vultures in Botswana

Human impacts on vultures can be severe (Boshoff *et al*. 1997), and even unintentional disturbance can be detrimental (e.g. Robertson 1984, Borello and Borello 1987b, 1992, Mundy *et al*. 1992). All vultures are protected by law in Botswana

(Ministry of Commerce and Industry 1992), but Mannyelanong is the only Cape Vulture colony in Botswana to have human access restricted by Government legislation (Ministry of Commerce and Industry 1985). Nevertheless, this has not prevented disturbance.

Mannyelanong Mannyelanong Hill was declared a Game Reserve in June 1985 and sanctuary fencing, which runs along the base of the scree slope below the cliff face and encircles the Cape Vulture colony, was installed in January 1986 (Borello 1986). In most years fledging success varied between 64% and 75% but in three years when excessive disturbance was known to occur, fledging success fell to 27–43%. In the middle of the 1992 breeding season the original fence was inexplicably removed and was replaced by another. During that year buildings were also erected at the bottom of the scree slope inside the sanctuary area. Fledgling productivity was low, despite above-average incidence of probable breeding (Table 7), and was most likely caused by this human disturbance during a critical period in the breeding season. Incursions by woodcutters well inside the sanctuary fence may have had a detrimental impact on the 1997 and 1998 breeding success. During the 1997 season sections of the fence were pulled down, particularly during the latter part of the breeding cycle. In May 1998 more of the fence was dismantled and there was evidence of intensive woodcutting and gathering inside the sanctuary, and felling of trees along the outside edge of the perimeter fence. On 23 September 1998 we found tracks of vehicles that had been backed up to the perimeter fence and evidence of large-scale removal of timber from inside the sanctuary. There was therefore strong evidence that the unusually high number of nest failures after laying, which for the first time exceeded the number of successful nests by mid season, can be ascribed to human disturbance. There had also been an increase in large groups of picnicking visitors (B. Kwambala, verbally). There was further evidence of woodcutting (July 1999) when mature live trees were removed. The Department of Wildlife and National Parks has now taken steps to prevent the incursions that probably contributed to the breeding failures in the late 1997 and mid 1998 season but sustained patrolling remains necessary, particularly over weekends.

Eastern Botswana Fledging success at Manong Yeng varied between 52% and 71%, but fell to 33–43.1% from 1997. The mid season success rate varied between 57.3% and 92.1%, but in 1997 fell to 40%. Sustained periods of human presence at the colony were known to occur throughout 1997, and also just prior to the young fledging in 1998 (e.g. Stevens and Ford 1999). By comparison, fledging success at Makoote-Sefhare in 1999 was 86.3%, a rate comparable with any southern African Cape Vulture colony when there is no interference.

Kukubye never had a high breeding success. Probably because of environmental factors and interference, numbers at the site had previously dwindled until the site was abandoned (Borello and Borello 1993). When most of the displaced Bonwalenong population resettled at Kukubye there was a strong likelihood that the population would fragment once more.

Currently there is an increase in the deforestation taking place on the lower scree slope at Kukubye, and the impacts of the 220 kV transmission line travers-

ing the base of the scree slope are unknown. We have never found any vulture strikes or electrocuted birds beneath the power line in front of the colony (the line has protective markers along that stretch), but it should be noted that no regular checks were made and scavengers may quickly remove dead birds. Although there are records of vultures being electrocuted when perched on 132 kV transmission line towers, probably caused when long streams of excrement induce a flash-over (van Rooyen and Taylor 1999), we have observed birds perched on the pylons on one visit only, in November 1995.

There is strong circumstantial evidence that human activities were a major contributory factor in the collapse of Bonwalenong. For decades the Bonwalenong colony was the most protected from human disturbance because of its hidden location in two intersecting gorges, and was known mainly to the local inhabitants only. Oral tradition has it that the gorge is ''The Home of All the Vultures''. We found and documented the colony in 1984. A later increase in human traffic affected birds breeding in one of the gorges, but by 1991 regeneration of the undergrowth inhibited access and again helped provide greater seclusion and the colony prospered (Borello and Borello 1992). Bonwalenong was considered the most likely colony to survive in the long term, provided it remained isolated from interference. Its collapse may have far reaching effects regarding the survival of Cape Vultures in Botswana. Unfortunately Bonwalenong has become increasingly advertised as a tourist attraction (Kalahari Conservation Society 1995, Hermans 1996). Although initially aimed at conserving the area and providing some revenue for depressed communities, efforts to start an ecotourism venture encompassing the Tswapong Hills have instead emphasized the establishment of the necessary infrastructures to encourage tourism. In the process the Cape Vulture colonies are losing their seclusion. A visitors' book in the village of Moremi bears testimony to the increase of tourists to the area, who are mainly attracted to the natural waterfalls that occur in one of the gorges. Among the criteria used to make an index of ''vulnerability'' for breeding colonies, Komen (1985) listed ''Habitat modification extensive, ongoing or imminent'' and ''Close proximity to recreational areas''. The risk of serious disturbance is not limited to Bonwalenong. At all colonies limiting the exposure of nestlings and juveniles to any form of disturbance is a key conservation objective (Scott 1997). An average of 75% breeding success (measured from eggs laid producing fledglings) is expected at undisturbed colonies, and it can be as high as 78–80% (Vernon *et al*. 1982, Donnay 1989, Scott 1997). The low success rates in the Tswapong colonies emphasize the vulnerability of those sites and should therefore be a cause for concern.

Disturbance by humans can be one of the main factors threatening the survival of Cape Vulture (e.g. Komen 1985, Scott 1997). Mannyelanong, Bonwalenong, and the remaining Tswapong sites are increasingly frequented by human traffic, while deforestation is taking place at Mannyelanong, and to a more alarming degree on the scree slope of Kukubye. It is inappropriate that breeding sites such as Tswapong are being promoted as tourist attractions and educational venues, and that people are also gaining uninhibited access into the protected area around the Mannyelanong cliff face. Urgent consideration is required as how to best protect one of Botswana's important bird species.

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W. D. BORELLO and R. M. BORELLO
P.O. Box 603, Gaborone, Botswana E-mail: borello@ sharps.co.bw

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