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Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents?

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The densities of self-established non-indigenous prickly pears (*Opuntia ficus-indica*) in rangelands of the Karoo recorded on 3434 km of road transects, were on average 800 times greater below telegraph and transmission poles than away from poles, and 200 times greater next to wire fences along roads than in open rangelands. We suggest that this uneven establishment pattern is mainly due to the dispersal of *Opuntia ficus-indica* seeds by crows and other vertebrates (chiefly primates). Cape (*Corvus capensis*) and pied crows (*C. albus*) feed on fruits of *Opuntia ficus-indica* in the Karoo, and regurgitate pellets containing viable seeds of these plants below nest sites, roosts and occasional perch sites. Crows use man-made structures such as wire fences, telegraph and transmission poles and windmills for perching, roosting and nesting. Crow pellets, containing regurgitated bones and viable seeds of *Opuntia* spp., and other alien and indigenous plants, are most common around such perch sites. Crows are frequently associated with roads in the Karoo because they scavenge on road kills in the Karoo as well as feeding on fruits, insects and reptiles in road verges. We suggest that dispersal of seeds by crows is important for range extension and establishment of new *Opuntia* populations.

Keywords: *Corvus*; semi-arid; avian frugivory; seed-dispersal

Introduction

The prickly pear (*Opuntia ficus-indica* L. (Mill.); Cactaceae) invasion of the early 1990s was one of the worst agricultural catastrophes in South Africa's history. The nuisance value and economic cost of impenetrable thickets of spiny cactus is reflected in the numerous popular and scientific articles that refer to the labour, herbicide and research invested in control during those years (Annecke & Moran, 1978). At the peak of the invasion, prickly pears reduced farming productivity and rural incomes so that some land owners abandoned their properties. Severe overgrazing by domestic livestock, as well as feral pigs and donkeys, occurred on the remaining usable rangeland.

A spineless form of the large succulent prickly pear was introduced to South Africa from the U.S.A. or Mexico in 1656 (Wells *et al.*, 1986), and was frequently planted in the semi-arid Karoo in the late 1700s, but by the late 1800s had become abundant in

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parts of the Karoo region (MacDonald, 1891), and by 1942 had covered about 900,000 ha in the Karoo and savanna of South Africa (du Toit, 1942). Spineless prickly pears are still being planted in the Karoo (Pretorius, 1986; le Houérou, 1994), and dispersal by frugivores is an additional factor affecting the spatial distribution and density of *Opuntia* spp. plants in the Karoo. There is convincing evidence that the spineless prickly pear gradually reverts to the thorny 'wild-type' which, being less favoured by herbivores, survives and spreads effectively to become a problem plant (Annecke & Moran, 1978).

In the drier parts of the low-altitude, largely treeless Karoo, this cactus is found mostly along river beds and road verges, but we suspect that this may be the result of directed dispersal of seeds, particularly by people, primates (*Papio ursinus* (Kerr) and *Cercopithecus pygerythrus* (F. Cuvier)) and birds (mainly corvids), rather than the inability of the plant to establish on open Karoo plains. Cape (*Corvus capensis* Lichtenstein) and pied crows (*C. albus* Statius Müller) are frequently associated with drainage line woodlands and roads in the Karoo (Siegfried, 1963; Winterbottom, 1975; Macdonald & Macdonald, 1983) because they scavenge on road kills in the Karoo as well as feeding on insects, reptiles and fruits in road verges and rangelands. Crows use man-made structures such as pylons and telegraph poles for perching, roosting and nesting (Siegfried, 1963; Winterbottom, 1975; Maclean, 1993; Malan, 1994). Crow pellets containing regurgitated bones and seeds are common below perch and nest sites (Skead, 1952; Brooke & Grobler, 1973).

In this paper, we show that prickly pear plants are associated with perch and nest sites commonly used by crows in the semi-arid Karoo, and suggest that the abundance and food of crows, and the perching and nesting sites used by crows are important factors in establishing patches of these plants.

Study site and methods

The Karoo consists of two biomes: the Succulent Karoo, primarily along the western and southern edges of the region, and the Nama Karoo in the remainder (Fig. 1). A broad description of the vegetation and other biota of the Succulent Karoo is given by Milton *et al.* (1998) and of the Nama Karoo by Palmer & Hoffman (1998). The Karoo region is largely treeless, except for narrow bands of trees (mainly *Acacia karroo* Hayne) along drainage lines and ephemeral rivers, and non-indigenous trees planted at roadside pulloffs and at farmhouses.

Road verges were surveyed on frequent trips to the southern and western parts of the Karoo and we recorded the numbers of corvids (cape and pied crows, and white-necked raven *Corvus albicollis* Latham) perching on fences or telegraph poles, nests in roadside trees and on telegraph poles, and recorded foraging behaviour and food of these birds from 1987 to 1999. A small sample of pellets was collected below crow roosts and perch sites. We examined the contents of pellets under a dissecting microscope and identified food items. Seeds from these pellets were germinated in wet sawdust.

In 1987, in a pilot study, we recorded the number of prickly pear plants along a 100 km stretch of road, and recorded the number of prickly pears that were associated with poles. In a subsequent study, in January 1998 we recorded all prickly pear plants within 100 m of one side of the road along three transects, and recorded the number of telegraph poles along transects and noted the number of prickly pear plants within a circle of 5 m radius centred on poles. All transects were done from a moving vehicle, and only plants larger than about 40 cm high were recorded. On 12 transects in January, February and April 1999, the counts were extended to include the number of prickly pear plants within 2·5 m either side of wire fences and the number of prickly pears growing on the road verge (between the road surface and fenced rangeland). It was assumed that a pellet regurgitated by a crow would fall within 2·5 m of a low perch

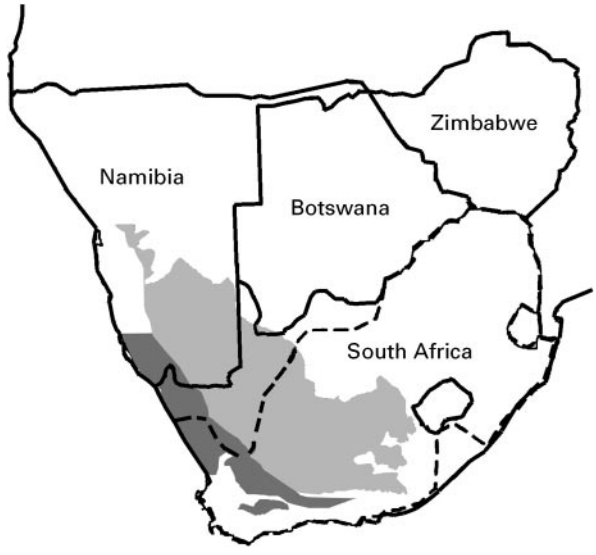

Figure 1. Southern Africa, showing the Succulent Karoo (dark grey) and Nama Karoo (light grey), and the distribution of *Opuntia ficus-indica* in South Africa within the dotted line (data from Henderson, 1995). This distribution is plotted at a $15' \times 15'$ scale, and masks the small high altitude gaps in the distribution of *Opuntia ficus-indica*. The gap in distribution in the eastern part of the Eastern Cape and western KwaZulu-Natal is probably a sampling artifact.

(a fence) or within 5 m of a high perch (a pole). The data were corrected for the area sampled, so that rangeland area sampled was (distance (km) $\times$ 100 m)/10,000 (= ha), pole area sampled was (number of poles $\times$ ($3{\cdot}1416 \times 5^2$ m))/10,000 (= ha) and fence area was (distance (km) $\times$ 5 m)/10,000 (= ha). The null hypothesis that prickly pears were distributed in the same proportions in all features of the landscape was tested using a Wilcoxon matched pairs test, and the proportion of nests on poles built by cape and pied crows using a Chi-squared test (Program Statistica 5.1, Stasoft Inc.).

Distribution of prickly pear in South Africa

In South Africa, overlays of climatic and topographic features on a recent quarter-degree distribution map (Richardson *et al.*, 1998) show that the prickly pear is most abundant at altitudes below 1400 m in summer-rainfall regions with a mean annual rainfall of 400–600 mm (or 60–80 rain days annually); on rocky substrata; at locations where it has a primarily eastern and southern distribution; and it is not common in the arid western interior of the Karoo (Henderson, 1995) (Fig. 1). *Opuntia* spp. appear to be limited by summer aridity in the winter-rainfall region and in the central Karoo, by freezing temperatures at high altitudes and by sandy substrates in the Kalahari. Plantations of spineless prickly pears are established from cladodes at altitudes from 1400 to 1600 m, and are used as fodder banks for sheep and cattle in dry and cold periods. Although there are large plantations of prickly pears on loams between Three-Sisters and De Aar in the eastern central Karoo, self-established plants are at very low densities in comparison with densities at lower altitudes (Table 1), probably indicating that the seedlings, rather than the adult plants, are frost-sensitive. The Kalahari region of the Northern Cape Province similarly has numerous small plantations of prickly pears and self-established plants also at a low density, but in this case probably due not only to the altitude and winter frosts, but also to the difficulties that the seedlings have in establishing on coarse sands.

Table 1. *Routes, altitude, soils, rainfall, distances and number of self-established* Opuntia *spp. (mostly* O. ficus-indica*) plants recorded. NC = no count*

Route (count no.)	Altitude (m)	Region	Soils	Rainfall (mm)	Distance (km)	Total *Opuntia* plants
Bloemfontein-Beaufort West (1)	400–1500	Karoo	loams	250–500	548	114
Colesberg-Bloemfontein (2)	1500	Grassland-Karoo	loams	500	228	28
Beaufort West-Leeu Gamka (3)	400	Karoo	loams	250–175	80	67
Prince Albert-Zeekoegat (4)	750	Karoo	loams	175	57	34
Zeekoegat-Beaufort West (5)	900	Karoo	loams	175–250	70	138
Beaufort West-Three Sisters (6)	1100	Karoo	loams	250	83	45
Three Sisters-Richmond (7)	1400	Karoo	loams	350	104	37
Richmond-De Aar (8)	1400	Karoo	loams	350	85	7
Beaufort West-Schoombee (9)	400–1000	Karoo	loams	350	367	335
Paterson-Schoombee (10)	200–1000	Karoo	loams	300–500	249	349
Three Sisters-Kimberley (11)	800–1500	Karoo-Kalahari	loams★	300–400	452	75
Kimberley-Kathu (12)	1500	Kalahari	coarse sands	400–500	281	51
Kathu-Tswalu (13)	1500	Kalahari	coarse sands	500–250	101	6
Tswalu-Molopo NR (14)	1500	Kalahari	coarse sands	250	285	0
Molopo NR-Kimberley (15)	1500	Kalahari	coarse sands	250–400	444	72
Total					3434	1358

★There is a gradient in soils from loams to coarse sands from south (Three Sisters) to north (Kimberley) along this transect.

Results

Prickly pears

Routes travelled, altitude, region, soils, rainfall, distance and number of *Opuntia ficus-indica* plants recorded along transects are given in Table 1. In our pilot study in 1987, 19 prickly pears were recorded along 100 km of highway between Prince Albert Road and Beaufort West, of which 13 were at the base of telegraph poles. In 1998–1999, of a total of 1385 *Opuntia* spp. seen along 3434 km of road, 306 were at the bases, or within 5 m of telegraph poles, 305 were within 2·5 m of fences, and the remainder in the road verge or in rangelands (Table 2). Correcting for area sampled gives a significantly higher density of *Opuntia* plants at the bases of poles ($z = 2{\cdot}84$, $p = 0{\cdot}004$) or next to fences ($z = 2{\cdot}93$, $p = 0{\cdot}003$) (Table 2).

Corvid density

Cape and pied crows are common in the Karoo *sensu lato* and occurred at a density of one crow for every 45·5 km travelled (523 cape and 934 pied crows counted in 66,414 km). White-necked ravens were generally at a low density, and only 146 individuals were recorded altogether. The behaviour, foraging, perching and nest sites of 1603 corvids (including ravens) in the Karoo are summarized in Table 3. Only cape and pied crows were recorded nesting on poles or in trees, and nests were more frequently on poles than in trees (Table 3). Nests of pied crows were disproportionately more common in general (76 nests)and significantly more frequent on poles ($\chi^2 = 8{\cdot}07$, $p < 0{\cdot}004$) than nests of the cape crow.

Seed dispersal

Corvid food items, including seeds, are given in Table 4. Crows feed on a variety of plants and animals, and seeds are regurgitated together with other indigestible parts of their food. Seeds are relatively infrequently found in pellets but occasionally are abundant, and appear to be viable. Pied crow pellets and pellet fragments (about six pellets in total) collected below a high-tension electricity pylon east of Beaufort West on 20 January 1998 contained, *inter alia*, 85 *Opuntia* seeds, 50 of which were planted on 26 January 1998, resulting in one *Opuntia* seedling. Pellet fragments (about 25 pellets) from a cape crow roost at Tierberg, east of Prince Albert, contained about 120 seeds of *Atriplex semibaccata* R. Br. and one *Euclea* sp. seed, as well as lizard and beetle remains. The *Atriplex semibaccata* seeds were planted in wet sawdust and produced 90 seedlings. Another collection of pellets and pellet fragments (about 500 g in total) collected from four roosts along the Prince Albert-Tierberg Road contained numerous fragments of animals (including arachnids, insects, lizards and tortoise remains) and seeds, including *Atriplex semibaccata*, *Diospyros* sp. (mainly *Diospyros lycioides* Desf., *Euclea undulata* Thnub., *Lycium* sp., *Opuntia* spp. (most likely *ficus-indica*) and *Thesium lineatum* L. f. (Table 4).

Discussion

Both cape and pied crows are reputed to have increased in numbers in the Karoo (Siegfried, 1963) and commonly make use of such man-made structures as windmills, transmission and telegraph poles for perch and nest sites (Siegfried, 1963; Jenkins & Underhill, 1997*a*, *b*). Our results support data presented by Siegfried (1963) who

Table 2. *Densities of* Opuntia *spp. (mostly* O. ficus-indica*) beneath poles and away from poles along five road-side transect strip counts (each 100 m wide) in the central Karoo in 1998. The area associated with telephone or transmission poles was calculated as a circle with a 5 m radius, the fence area calculated as a strip 5 m wide (see Methods), and the rangeland area was calculated as the area of rangeland less the pole area. All areas given in ha. NC = not calculated*

Route	Rangeland area	No. poles	Pole area	Fence area	*Opuntia* in rangeland		*Opuntia* at base of poles		*Opuntia* next to fences	
					No.	Density (no. ha^{-1})	No.	Density (no. ha^{-1})	No.	Density (no. ha^{-1})
1	5469·24	5480	10·8	27·4	51	0·01	5	0·5	53	1·9
2	2275·52	2280	4·5	11·4	1	0	0	0	25	2·2
3	798·43	800	1·6	4	19	0·02	20	12·7	21	5·2
4	569·1	570	0·9	NC	30	NC	4	6·0	NC	NC
5	698·9	700	1·1	NC	109	NC	29	19·7	NC	NC
6	1138·21	1140	1·8	NC	25	NC	20	5·4	NC	NC
7	159·75	160	0·3	NC	37	NC	0	3·6	NC	NC
8	848·66	850	1·3	NC	7	NC	0	0·8	NC	NC
9	3662·79	3670	7·2	18·4	64	0·02	100	13·9	78	4·2
10	2485·11	2490	4·9	12·5	93	0·04	99	20·3	81	6·5
11	4511·12	4520	8·9	22·6	12	0	18	2·0	21	0·9
12	2804·48	2810	5·5	14·0	28	0·01	1	0·2	10	0·7
13	1008·02	1010	2·0	5·0	4	0	0	0	1	0·2
14	2844·4	2850	5·6	14·2	0	0	0	0	0	0
15	4431·28	4440	8·7	22·2	21	0	10	1·2	15	0·7
Totals	33,705	33,770	65·1	108·9	501	0·11	306	86·3	305	13·2

Table 3. *Numbers of crows (Corvidae) and their activity, behaviour and nest sites recorded along roads in the Karoo. The category 'flying' includes birds flying along the road as well as over rangelend adjacent to the road*

Distance (km)	Crows	Dead on road	Flying	Foraging				Perching			Nesting	
				On road	In verge	At pulloff	In rangeland	On fence	On pole	On tree	On pole	On tree
66,414	1603	6	558	95	150	23	122	72	445	26	117	15

Table 4. *Food items found in corvid pellets (mainly cape crow* Corvus capensis*) (approximately 300 pellets, 500 g pellet mass in total) collected from below five roosts and five nests randomly encountered in the Prince Albert-Beaufort West area of the Karoo, South Africa. The* 'n' *for animals is the minimum number of pellets containing the particular food item, and for plants is the total number of seeds from all pellets. All pellets examined contained various amounts of unidentifiable fibrous material, probably of plant origin*

Animals

Food item	*n*
Millipedes	6
Snail or crab shell	5
Solifuges	3
Termites (mouthparts)	1
Beetles (Curculionidae)	53
Beetles (Probably Tenebrionidae)	58
Moth pupae (cocoons)	6
Ants	2
Tortoise shell	2
Tortoise hatchling (complete)	1
Lizards	26
Mammal bones	10
Mammal skin	1
Mammal hair	6 +

Plants

Food item	*n*
Atriplex semibaccata	120 +
Diospyros sp.	267
Euclea undulata	26
Lycium sp.	228 +
Opuntia (probably *ficus-indica*)	86
Thesium lineatum	1
Mesembryanthemum seed capsule	1

shows that nests on poles and windmill platforms are far more frequent than nests on trees in three magisterial districts in the Karoo. About 60% of both cape and pied crow nests recorded by Siegfried (1963) were on windmill platforms or telegraph poles, and the remainder on trees, bushes or cliff ledges. This disproportionate use of man-made structures for nest sites implies that crows have extended their breeding range in the Karoo, although this may be an artifact of the data set — nests on poles and windmills are more visible than nests on trees or bushes.

Pole-nesting and the discarding of food remains at perch and nest sites, however, have consequences for seed dispersal and survival of certain plants. Cape crows feed on a variety of juicy fruits, including *Scutia myrtina* (Burm. f.) Kurz., *Diospyros* spp. (including '*Royena pubescens*'; Skead, 1952), *Euclea* sp. and *Lycium* spp (Skead, 1952; Table 4). Cape crows also feed on *Opuntia* spp. and Skead (1952) noted that the birds remove the fruit pulp and seeds from the fruit *in situ*. Published records of food of the pied crow suggest that juicy fruits are less frequently eaten than dry seeds (Siegfried & Grindley, 1967; Brooke & Grobler, 1973). We have recorded both cape and pied

crows feeding on *Opuntia* fruits in the Prince Albert area and other parts of the Karoo (WRJD & SJM, pers. obs). The numbers of seeds in pellets (Skead, 1952; this study) suggests that the birds are effective dispersers of juicy fruited plants, although many seeds may be deposited in exposed sites below poles or windmills that are unsuitable for the survival of indigenous plants. However, Skead (1967) suggests that the bases of telegraph poles function as 'nurses' (see, for example, Cody, 1993; Hacker & Gaines, 1997) and are important establishment sites for several indigenous and alien plant species in the Eastern Cape.

Our observations suggest that prickly pears can establish and survive at the bases of telegraph poles and along wire fences and by so doing can extend their distribution into rangelands in the Karoo. There are no published data on the foraging ranges of cape and pied crows (although nests may be fairly closely spaced; Malan, 1994), but both species are powerful fliers and can probably disperse seeds far from mother plants. Once prickly pears become established in isolated patches in rangeland, sub-populations of this plant become self-reinforcing, by providing fruits that are eaten by crows and other animals and further dispersed to other sites in the rangeland. Chacma baboons feed on *Opuntia* spp. fruits (Smithers, 1983) and in the more mesic eastern Karoo it is likely that baboons and possibly vervet monkeys are efficient dispersers of prickly pear seeds. Both baboons and monkeys sit on top of telegraph poles, pylons and on wire fences, as well as on rocks and trees (Smithers, 1983; WRJD & SJM, pers. obs). One other frugivorous bird may also play a minor role in the dispersal of prickly pears in the Karoo. The African pied starling *Spreo bicolor* occurs throughout the Karoo (Maclean, 1993), and includes fruit in its mixed diet. This starling frequently perches on fences and poles in the Karoo, but nests in holes in earth banks or buildings. We have never observed African pied starlings feeding on prickly pear fruits, but it is quite likely that they do so. However, we have no records of prickly pear plants germinating at the bases of earth banks below starling nests, and we consider it unlikely that the African pied starling plays any, other than a very minor role, in the dispersal of prickly pears in the Karoo.

The cochnineal insect *Dactylopius opuntiae* (Cockerell), was introduced in 1938 as a biocontrol agent and by 1946 had substantially reduced the density of cactus. As Zimmermann *et al.* (1986) have pointed out, the present distribution of prickly pear in South Africa reflects the success of this biocontrol agent, as well as the response of the cactus to the environment. The cochineal insect that has maintained prickly pears at low to moderate densities since the mid 1940s, is particularly effective in hot arid areas. Wetter conditions limit the fecundity of this wind-dispersed insect (Zimmermann *et al.*, 1986), and would therefore enable prickly pears to expand in range and increase in density in the Karoo if there is an increase in rainfall as a result of global climatic change. Increases in roads, over-land electricity cables, human population, primates and crows are all likely to facilitate the spread of *Opuntia ficus-indica* and other Cactaceae, but regardless of global change and landuse scenarios, high altitude and deep sandy areas will probably always remain free of prickly pear plants.

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