What precipitates influxes of wetland birds to ephemeral pans in arid landscapes? Observations from Namibia

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The ability of wetland birds to rapidly find and exploit ephemeral pans is well known in arid lands, but the episodic nature of such events means that the methods employed are poorly understood. Birds may: (i) wander randomly until wetlands are found; (ii) predict rainfronts and rainfall using changes in pressure gradients as cues; or (iii) follow rainfronts directly and descend onto pans as they fill. Observations from isolated pans in Namibia during the first rains indicate that wetland birds follow rainfronts, and descend onto pans as they fill. In one 30 ha pan, 37 birds of 5 species had arrived one day after filling and in another 50 ha pan over 300 birds of 13 species were attracted within 3 days of filling. Wetland birds, like migratory raptors, therefore, follow rainfronts, and may wander locally thereafter. How species such as grebes and flamingos that exploit these pans for later breeding and intercontinental movements (respectively) time their flights to coincide with fully flooded pans remains unknown.

INTRODUCTION

Anecdotes abound in southern Africa of the ability of birds to travel long distances to find and exploit ephemeral pans in arid regions. Among some Anatidae for example, ringing studies have shown that species such as Redbilled Teal *Anas erythroryhcha* and Knobbilled Duck *Sakidiornis melanotos* regularly move between 240 and 2 000 km between wetlands (Oatley & Prys-Jones 1986). However, because of their sporadic nature, research has been unable to quantify the cues used by wetland nomads such as these and their remarkable ability to find highly isolated and temporary wetlands in vast arid landscapes. The most intriguing example from Namibia, sub-Saharan Africa's most arid country, is the ability of both species of flamingo *Phoenicopterus ruber* and *Phoeniconaias minor* to time their flights from their wintering areas on Namibia's desert coast to coincide with flooding of their main breeding site in Etosha Pan 500 km north-east (Etosha Ecological Institute staff, unpubl. data). Birds leave the coast only when Etosha has had substantial rain (Williams & Velasquez 1997), yet they do not directly experience any rainfall, and rely on an unknown cue to time their flights inland (Simmons 1997). These species are the most puzzling example along a continuum that extends to wetland birds that may follow such cues as rain fronts or regularly sample neighbouring wetlands for their suitability.

Three possible methods could be used by birds to locate wetlands in arid environments: (i) birds regularly sample ephemeral wetlands, covering large areas, without observers realising they do so, or (ii) birds rely on rain-associated environmental cues such as changes in pressure or temperature allowing them to predict future flooding (J. Mendelsohn, pers. comm.), or (iii) they follow large scale rain fronts as do some migrant raptors (Steyn 1982), arriving as wetlands are filling. We report here observations from three ephemeral pans in northeast Namibia's Tsumkwe district (hereafter Bushmanland) that provides evidence supporting one of these possibilities.

STUDY AREA AND METHODS

Observations were made in north-eastern Namibia's Bushmanland Pans before, during and after thunderstorms that filled three endorheic pans there in 1996-1997. These pans occur in well wooded bushy areas on Kalahari sand and calcrete, and are well known for their rich and diverse avifauna (Jones 1988; Mendelsohn & Ward 1989; Hines 1993). Rapid movements into and explosive breeding thereafter are similar to that recorded in the better known Nylsvlei floodplain in northern South Africa (Dennis & Tarboton 1993). The pans fill with local rains and in exceptional years (total rainfall > 1000 mm) remain flooded until the next season's rain which generally start in October. However, evaporation rates are high at about 2.8 m per year ensuring that the pans are usually dry again before the next rains. Mean rainfall is 450 mm and is highly variable: seasonal rains between October and April vary from 110 mm to 1200 mm per season (Hines 1993). Rainfronts approach from the north and northeast as the zone of intertropical convergence moves south as the season progresses. Timing is also highly variable and the first rains may arrive in August or as late as December. Our main observations concern two small isolated pans 20 km north of Tsumkwe at Klein Dobe (19°25.6' S, 20° 33.2'E), and Groot Dobe (19°25.2'S, 20°35.8'E). Additional observations were made from the largest pan in this area at Nyae Nyae (*c.* 2.5 km^2), 18 km south of Tsumkwe (Fig. 1). These pans, 30 and 50 ha in area respectively, are largely unvegetated, shallow, fresh water, clay pans, circular in nature, completely surrounded by woodland and 4.6 km apart. The pans are isolated from the Nyae Nyae Pan to the south by about 38 km and the closest major wetlands occur on the eastern edge of Okavango Swamps, about 180 km due east. Further descriptions of all the pans are given by Hines (1993). We revisited the pans 2 months later in late February to determine the status of wetland birds.

RESULTS

Rainfall

Our first visits to the pans occurred on 26 December 1996, before any substantial rains. Rainfall over the previous 2 months had totalled about 60 mm and only Gautcha Pan (40 km south) and about 20% of the surface area of Klein Dobe Pan held any water. All other pans were dry and no birds were present. Violent storms were recorded on 27, and 28 December, with further rain on 29 December, but none immediately thereafter. This is a typical start to early rainfall in Namibia, and rapid flooding is not unusual following such events (Schalk 1961).

Table 1. *Increase in bird numbers and species before and after rains on Klein Dobe and Groot Dobe Pans over a 6 day period, December, 1996. Day 1 = 26 December, Day 6 = 31 December. No rain occurred on days 1, 5 and 6. Storms occurred on days 2 and 3, and steady rain on day 4.*

Species	Klein Dobe Days						Groot Dobe Days					
	1	2	3	4	5	6	1	2	3	4	5	6
Saddlebilled Stork *Ephippiorhynchus senegalensis*	0	1	1	1	-	0	-	-	-	0	0	0
Marabou Stork *Leptoptilos crumeniferus*	0	0	0	0	-	2	-	-	-	0	0	0
Yellowbilled Stork *Mycteria ibis*	0	0	0	0	-	9	-	-	-	0	9	0
Openbilled Stork *Anastomus lamelligerus*	0	1	1	0	-	0	-	-	-	0	0	0
Greater Flamingo *Phoenicopterus ruber*	0	0	0	0	-	0	-	-	-	0	67	0
Lesser Flamingo *Phoeniconiais minor*	0	0	0	0	-	0	-	-	-	0	6	4
Redbilled Teal *Anas erythrorhynca*	0	0	30	38	-	60	-	-	-	54	45	12
Knobbilled Duck *Sarkidiornis melanotos*	0	0	0	1	-	0	-	-	-	0	0	0
Glossy Ibis *Plegadis falcinellus*	0	0	4	0	-	0	-	-	-	4	4	0
Spoonbill *Platalea alba*	0	0	0	0	-	2	-	-	-	0	1	1
Yellowbilled Egret *Egretta intermedia*	0	0	1	1	-	0	-	-	-	0	0	0
Cattle Egret *Bubulcus ibis*	0	0	0	0	-	0	-	-	-	15	12	3
Greyheaded Gull *Larus cirrocephalus*	0	0	0	0	-	7	-	-	-	0	0	0
Whitewinged Tern *Chlidonias leucopterus*	0	0	0	1	-	0	-	-	-	0	0	0
Whiskered Tern *Chlidonias hybridus*	0	0	0	3	-	0	-	-	-	0	8	0
Blackwinged Stilt *Himantopus himantopus*	0	0	0	4	-	6	-	-	-	2	4	0
Avocet *Recurvirostra avosetta*	0	0	0	0	-	13	-	-	-	5	14	20
Blacksmith Plover *Vanellus armatus*	0	0	0	10	-	4	-	-	-	0	0	0
Common Sandpiper *Actitis hypoleucos*	0	0	0	0	-	0	-	-	-	0	2	0
Wood Sandpiper *Tringa glareola*	0	0	0	0	-	4	-	-	-	0	2	0
Marsh Sandpiper *Tringa stagnatilis*	0	0	0	1	-	0	-	-	-	0	0	0
Greenshank *Tringa nebularia*	0	1	0	10	-	11	-	-	-	5	11	1
Ruff *Philomachus pugnax*	0	0	0	0	-	0	-	-	-	0	14	0
Number of birds	0	3	37	70	-	118	-	-	-	86	326	21
Number of species	0	3	5	10	-	10	-	-	-	7	13	5

Klein Dobe Pan

The thunderstorm that struck the area on the afternoon of 27 December filled the pan to an estimated 90% full within 2 hours. The water reached 25 m from the edge and was about 30 - 40 cm deep. During the storm birds began to arrive: one Saddlebill Stork *Ephippiorhynchos senegalensis*, one Open billed Stork *Anastomus lamelligerus*, one Greenshank *Tringa nebularia* and 4 Crowned Plovers *Vanellus coronatus* were observed (Fig. 1) on the pan. We exclude the latter species in further analyses since they are not strictly wetland species.

Drizzle during the night followed by another thunderstorm on 28th December led to further filling and an increase in the radius of water by 5 m. A count the same day revealed 37 birds of 5 species (Table 1). Total rainfall for the two days was about 35 mm in Tsumkwe (N. Berriman pers. comm.). A third count (29 December) two days after the first storm, revealed 73 birds of 11 species - a doubling of species richness and abundance in a day (Fig. 1). The highest total was observed 5 days after the storm (the last day of counts) when no further rain had fallen (Table 1). Thus in 5 days, the filling of the Klein Dobe pan attracted 118 birds of 10 species. Two months later, Klein Dobe had the same amount of water, was 40% grass (*Diplachne fusca*) covered and supported 107 birds of 7 species, including six Wattled Cranes *Grus carunculata*.

Groot Dobe Pan

Groot Dobe, a larger, more saline pan, which is often dry (Hines 1993), was first completely sampled a day after the rains had finished on 29 December, when a shallow layer of water, 1 - 3 cm deep, was present on the largely unvegetated pan. It had few birds (<10) a day earlier when we made a casual visit and incomplete count (Table 1). Our first count revealed the same order of magnitude of birds (86) as found at Klein Dobe on the same date (29 December) and comprised mainly Redbilled Teal *Anas erythrorhyncha* (54), in a total of seven species (Table 1). The peak number of birds occurred a day later (30 December), when 326 birds of 13 species were present, swollen by the temporary presence of both species of flamingo (73), and Avocets *Recurvirostra avosetta* (142), some of which were copulating. Birds declined thereafter on our last count (Fig. 1), when the pan had little remaining water. Observations two months later in the last week of February indicated that Groot Dobe was dry and covered in grass with no birds.

Nyae Nyae Pan

On 28 December we visited Nyae Nyae, a large mainly unvegetated pan, known to hold water longer than most other pans in the area. It was dry but rain was falling to the north. On 30 December approximately 100 flamingos of both species were seen exploiting the small surface area of water (< 1 ha) that had formed. These birds appeared to commute back and forth between Groot Dobe (38 km north) where we counted 73 birds late on 30 December. The next morning they had gone and only three remained at Nyae Nyae. One hour before sunrise on 1 January 1997 about 40 flamingos flew from the western horizon, circled Nyae Nyae, and disappeared in a northeasterly direction. Of 11 species of raptorial bird seen at the same time, thousands of Western Red Footed Falcons *Falco vesperinus* descended on the Nyae Nyae area, on the last day during thunder activity.

DISCUSSION

The ability of birds, particularly wetland species to find ephemerally flooded wetlands in vast arid landscapes has been verbally noted many times by southern African ecologists. How birds manage to find these small wetlands has been difficult to determine because of the episodic nature of such events, and the low observer density in arid lands. We have shown here that wetland birds do indeed have a remarkable ability to quickly find ephemeral pans within hours of filling and they do so, not by haphazardly searching, but

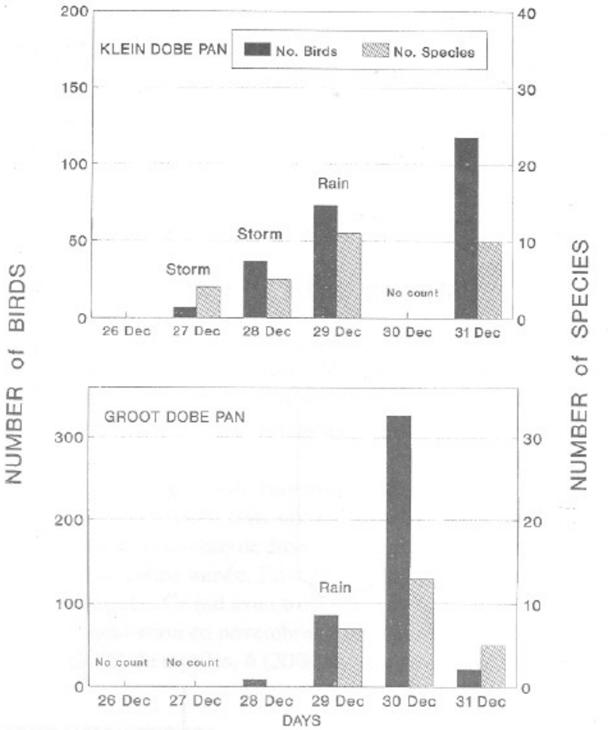

Fig. 1. Increase in abundance and species richness of wetland birds with rainfall on two isolated pans in Bushmanland, Namibia. The top graph indicates complete counts during and after storm weather at the 30 ha Klein Dobe Pan, and the bottom graph shows increases at the 50 ha Groot Dobe Pan sampled 3 days after the first storm weather.

travelling with the storm and arriving as the first rains fill the pans. That they continued to arrive as further rains occurred suggests several waves of arrival. This continued arrival does not rule out the possibility that other pans that were full (e.g. Gautcha Pan) were sampled first, and birds then moved to less disturbed habitat at Groot and Klein Dobe. That this is not unique to birds in Namibia is suggested by the observations of Taylor (1985;1987 and unpublished) who recorded flufftails (*Sarothrura* spp.), crakes (*Porzana* and *Crex* spp.) and snipe (*Gallinago* spp.) arriving in damp grasslands in Zambia and Kenya within 12 -24 hours of heavy rain or storms. They were not recorded at other times during intensive field studies indicating that these species too were responding rapidly to the storm event and not merely calling or displaying in response to rain.

The adaptive advantage of arriving shortly after flooding is presumably related to the other ecological events triggered by the rains, namely the emergence in massive numbers of frogs, termites and dragonflies that have lain dormant in and around such temporary pans. Invertebrate fauna also quickly hatch and develop in the temporary pools (Kok 1987) adding to the diversity. This temporary abundance of resources provides food to wetland and raptorial birds (pers. obs.), some of which immediately begin to breed. Breeding species in Bushmanland include the ducks, terns, avocets and stilts given in Table 1, while later breeders which arrived after this first wave include colonial nesting Redknobbed Coots *Fulica cristata*, Lesser Moorhens *Gallinulla angulata,* Baillon's Crakes *Porzana pusilla* and Slaty Egrets *Egretta vinaceigula* (Jamieson *et al.* MS). Given that temporary pools can quickly dry under the intense evaporation levels apparent here, early arrival and exploitation is clearly adaptive behaviour. The colonial nesting species, however, require deep-water conditions with associated grass cover, which was not present immediately after the first rains. This may explain why such species did not arrive at the same time, but were present in their hundreds 2 months later (Jamieson *et al.* MS).

The 23 species of wetland bird that arrived within 5 days of the first substantial rains at Groot Dobe pan, represent 47% of the total wetland species (excluding charadrii waders and passerines) recorded from here (Hines 1993). Four species of stork were seen in this time, to which Wattled Crane and Slaty Egret were important additions by the following February. The overall importance of these pans may be gauged from the peak total of 11073 birds (of 37 species) present on Nyae Nyae Pan during 7 year's monitoring (Simmons 1992).

Long distant migrants such as kites *Milvus* spp.and kestrels appeared with the same rain event indicating that ecologically different taxa exploit the larger rain fronts that meet certain threshold conditions (size or pressure gradient). The rain not only fills temporary pans but stimulates termite (*Hodotermes* spp.) alates to emerge (Jensen 1972, Hines 1989), a major food source for many migratory raptorial birds. Satellite tracking of a Lesser Spotted Eagle *Aquila pomarina* moving with rainfronts in southern Africa showed a massive range of 25 000 km^2 (Meyburg *et al.* 1995), indicating large (± = 250 km/day) movements in search of suitable habitat.

Our observations do not rule out the third option that birds predict when rain fronts occur with cues such as changes in air pressure or temperature. This may not be necessary, however, since the thunder heads that developed north of Bushmanland and swept south were visible for tens of kilometres and, to a bird soaring to the north at several hundred metres, possibly from hundreds of kilometres. How birds that require well flooded pans for breeding after the rainfronts have passed (flufftails, rallids and grebes) time their arrivals is unknown, but they may simply wander large distances as suggested by unusual occurrences of flufftails in Namiba (Simmons 1996) and elsewhere (Taylor 1997). Certainly some Anatidae regularly move large distances, with Redbilled Teal exhibiting wide scale movements in southern Africa with median distance of movement (ringing to recovery) of 244 km, and 10% of 77 recovered Knob-billed Duck *Sakidiornis melanotos* exhibiting movements of over 2 000 km (Oatley & Prŷs-Jones 1986).

For flamingos our observations of their temporary use of the two pans, and their disappearance north-eastwards suggests that the Bushmanland Pans are a convenient stopover for birds that cover about 600 km in a night (Williams & Velasquez 1997), moving from the Etosha Pan. Etosha (380 km west) was flooded at this time but supported few flamingos (P. Stander pers. comm.) while Sua Pan in Botswana, 980 km due east, which had supported breeding flamingos the year before, may have been their final destination. It too was flooded and birds attempted breeding there in March 1996 (T. Liversedge pers. comm.). Up to 6 000 Lesser Flamingos have used these small pans for short periods in other years (Hines 1989), supporting the idea they may be a regular stopover. What remains puzzling is how these birds, which live on the western coastal edge of the Namib Desert, thousands of kilometres from north-south moving rainfronts, time their migrations to coincide with flooding inland. Satellite monitoring of their movements and laboratory experiments on the ability of these birds to hear low frequency sounds from thunderstorms may be instructive.

We conclude that the remarkable ability of wetland birds to find and exploit ephemeral pans in arid landscapes is due in part to their behaviour of directly following massive thunder heads and arriving as temporary pans are filling beneath them. In this respect they behave no differently to raptorial species (Steyn 1982) and derive similar (food) benefits.

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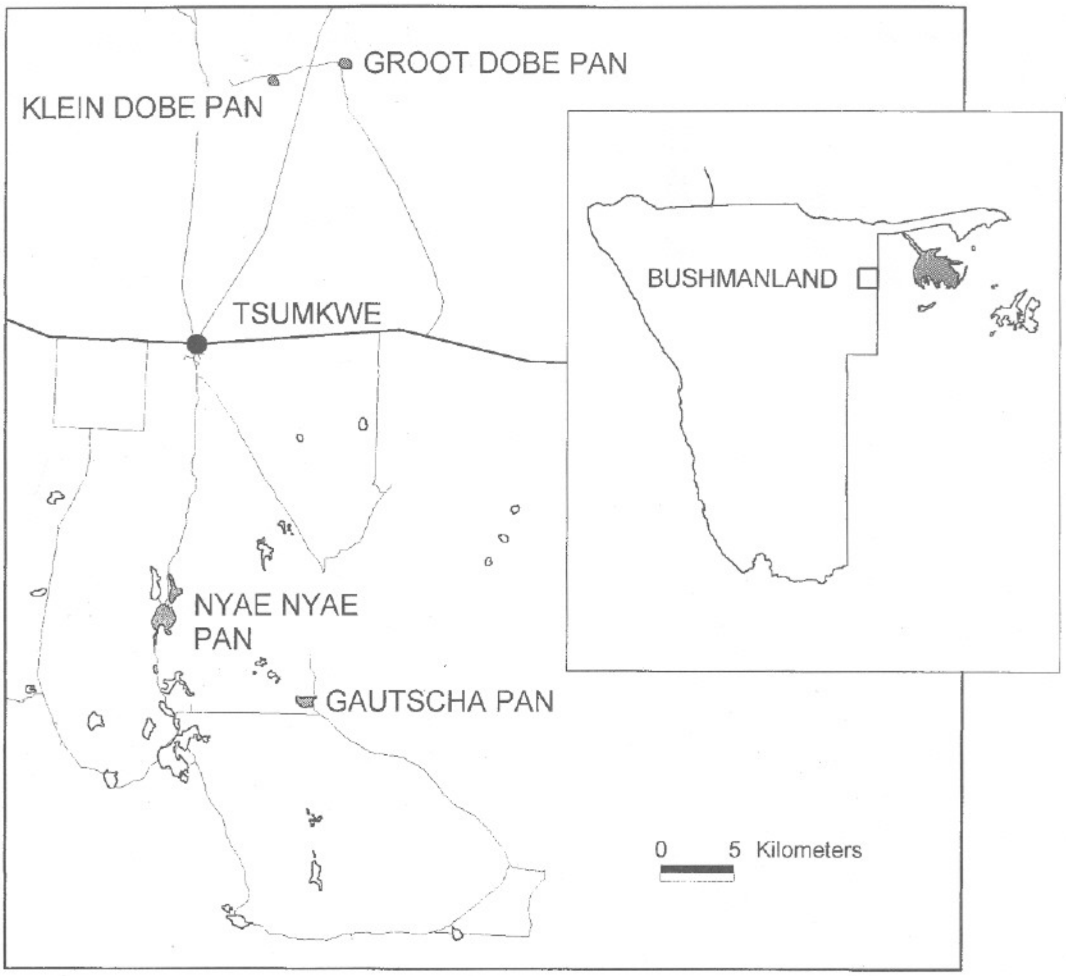

Fig. 2. The location of ephemeral pans in Bushmanland, northeast Namibia, indicating those that were flooded (dark) and those that were dry in December 1996. The nearest permanent natural wetland, the Okavango Swamps (180 km east) is shown for comparison.

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