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THE EFFECT OF PRIMARY PRODUCTION ON BREEDING SUCCESS AND HABITAT SELECTION IN THE AFRICAN HAWK-EAGLE[1]

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Abstract. Breeding success of 116 African Hawk-Eagle, *Hieraaetus spilogaster,* pairs nesting on basalt (4,724 km^2—63 pairs) and kalahari sand (9,876 km^2—53 pairs) was monitored from 1973 to 1984 in Hwange National Park, Zimbabwe. Nest-tree choice on both biomes was determined by the most abundant large trees; flat-crowned thorn trees on basalt and round-crowned rough barked trees on sand. Mean internest distances between biomes were significantly different (4.74 km [basalt], 8.65 km [kalahari sand]). Most clutches were laid in May and June and more one-egg clutches were recorded on sand. Breeding success, laying dates, and clutch size were all affected by rainfall. Greater success, early laying, and large clutch sizes were recorded during the period of higher rainfall, 1973 to 1976 (mean annual rainfall 783 mm) as compared to 1979 to 1984 (mean annual rainfall 601 mm). More breeding attempts took place in open woodland than closed woodland, but there was no difference in the number of chicks produced in both areas.

Key words: Primary production; breeding success; habitat selection; African Hawk-Eagle; Hieraaetus spilogaster; *afrotropics.*

INTRODUCTION

The structure of any ecological community is determined by the balance between the availability of water and soil nutrients (Bell 1982). Primary production is greatest where light, warm temperatures, water, and mineral nutrients are all abundant (Ricklefs 1979) and is dependant to some extent on soil type, particularly its water, mineral, and nutrient retention. Rutherford (1978), in one review of southern African soil productivity, reported higher primary production on soils with a high clay content while sandy soils had a lower productivity. Differential soil productivity results in differences in primary production which would affect consumers living in the various trophic levels in these areas. It follows that we should expect to find more consumers on highly productive soils when compared with less productive soils.

Newton et al. (1977) found Eurasian Sparrowhawk, *Accipiter nisus,* nesting territories to be evenly spaced, but at varying distances which were related to soil productivity (as measured using a land productivity index), altitude, and in three measured cases, to the abundance of small bird prey. In one valley, sparrowhawks nested more densely on the richest ground close to the coast, at intermediate densities half way up the valley, and at lowest densities at the top of the valley on poor ground. Ratcliffe (1969) found Peregrine Falcon, *Falco peregrinus,* pairs closer together in areas of good land productivity and food, even though food was not directly measured. Black Eagle, *Aquila verreauxi,* pairs were closer together where outcrops were close together (and therefore more hyrax *Procavia* sp. prey) than pairs in areas where the outcrops were further apart (Gargett 1975).

Clay-derived soils on a basalt substrata have better water and nutrient retention than sand-based soils of aeolian origin which make up the soils in the kalahari sand part of Hwange National Park. We examined breeding parameters and success of 116 African Hawk-Eagle, *Hieraaetus spilogaster,* pairs nesting on basalt and kalahari sand substrata in the Hwange National Park (26°30′E, 19°00′S), Zimbabwe, to determine the influences of differing primary production on aspects of their breeding biology and success.

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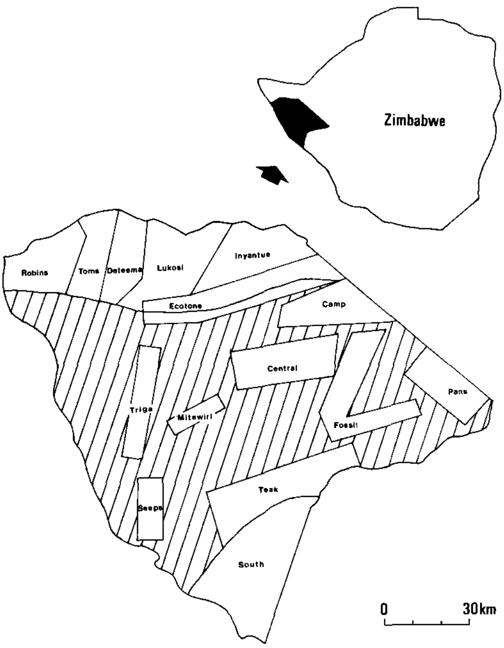

FIGURE 1. Map of Hwange National Park, showing location within Zimbabwe, basalt (unhatched) and kalahari sand (hatched) biomes and nesting districts.

STUDY AREA

The 14,600-km² Hwange National Park in northwestern Zimbabwe (Fig. 1) comprises three physiographic areas: two on basalt and one on sand.

The northern basalt area varies from hilly and broken country in the north and east to undulating seasonally wet vleis (grasslands) in the west. Shallow soils predominate except along drainage lines which support well-developed *Acacia* riparian communities. Vegetation on the northern basalt is almost entirely mixed woodland dominated by *Colophospermum mopane*; the woodland is stunted and not as dense in the west, becoming thicker and taller in the east. The southern low lying basaltic flats support seasonally inundated *C. mopane* woodland and scrub. The combined basalt areas comprise 4,724 km² (32%) of the park surface area.

Aeolian kalahari sands comprise the remaining 9,876 km² (68%) of the surface area with a generally flat topography. The main vegetation is *Baikiaea plurijuga* woodland interspersed with *Terminalia sericea* scrub. Drainage lines, which flowed during prehistoric times, bisect the area and have well-grassed centers and are fringed by well-developed *Acacia erioloba* woodland. Calcrete underlies the sands on the ecotone, supporting grasslands with scattered scrub and seasonal pans during the rains.

STUDY POPULATION

The African Hawk-Eagle is a medium-sized eagle (males weigh 1,250 g, females 1,580 g; Maclean 1984) living in woodlands over much of Africa; it does not inhabit forest and open savanna (Steyn 1982). It is a rapacious hunter and eats birds (75% of recorded items of which 70% were gamebirds) and mammals (most [50%] of which were bush squirrels) (Steyn 1982, Tarboton and Allan 1984). The Hwange National Park population consists of resident territorial breeding adults and an unknown number of nonbreeding adults and immature birds.

METHODS

A fixed-wing aircraft was used to check each nest at least twice during the breeding season (April to October) from 1973 to 1984. Flights were timed to give information on the fate of clutches and small young (May) and the outcome of the breeding attempt (October). Nest positions were marked on a 1:50,000 map which was carried in the aircraft. Breeding sites used the previous year were visited first. If they were unused we checked known alternate sites or searched for new ones in the vicinity of known nests of the pair concerned. Local weather conditions, especially wind, determined flight times, areas visited, and the number of pairs checked on any flight. The 1977 and 1978 nest checks were incomplete and have been omitted from this analysis.

We categorized nests as no breeding attempt, nest building, eggs laid, chicks hatched, or nest successful as previously described (Hustler and Howells 1986). For this study only known breeding attempts have been considered and the outcomes split into successful or unsuccessful. Approximate egg-laying dates were obtained using relative feather development of chicks following information in Steyn (1975). An incubation period of 43 days (Steyn 1982) was used in these calculations. Chicks older than 49 days were considered to have fledged successfully if the nest was not revisited. The total fledgling period is about 65 days (Steyn 1982) so chick mortality figures may slightly underestimate the true mortality figure.

Nests were grouped into those on basalt (63 pairs) and kalahari sand (53 pairs). Information on terrain and vegetation characteristics in the vicinity of the nest were recorded in order to determine their influence on breeding performance and productivity of African Hawk-Eagle pairs. Internest distances were measured from the 1:50,000 map. Nests, where the next neighbor could not be easily confirmed were excluded from the analysis. Analysis of breeding data was clumped into two periods; 1973 to 1976 and 1979 to 1984 on the basis of the differing mean annual rainfall (783 mm vs. 601 mm) recorded during these periods respectively.

We described nest trees as (1) flat- or round-crowned and (2) thorny or smooth bark, to investigate nest-tree characteristics. Nests found in the same general area of a known geographical landmark or in the same drainage basin were grouped; boundaries of these have been smoothed to ease illustration (Fig. 1). No account of ecological differences between nests within each group was taken and there may be differences in the characteristics of each area which may affect breeding success. The mean number of breeding attempts and success of pairs nesting there was calculated. Means were multiplied together to determine the most productive areas in the park, in terms of numbers of young African Hawk-Eagles produced.

RESULTS

NESTING HABITAT, TOPOGRAPHY, TREE TYPES AND INTERNEST DISTANCES

Fifty-two percent of the nests ($n = 63$) on basalt were located in *Acacia* riparian woodland and 37% in mixed woodland. There was no significant difference in breeding success of these pairs ($\chi^2 = 0.02$, $P > 0.05$). Ninety-five percent of all known pairs ($n = 63$) were found along rivers and 68% of pairs bred on small hilly tributaries of the main drainages of the area.

Pairs nesting on Kalahari sand were mainly in *Baikiaea* (68%, $n = 53$) or mixed woodland (32%). Breeding success in both vegetation types was similar ($\chi^2 = 0.03$, $P > 0.05$). Most pairs nested on nondescript flat terrain (96%, $n = 53$) with the remaining pairs nesting close to a fossil drainage line.

Ninety-four percent of all known nests were found in 70% of the habitat types available. Similarly, 84% of known nests occurred on 90% of the topographical features of the park, suggesting that African Hawk-Eagles are distributed evenly throughout the park.

Most nests on basalt were in flat-topped trees with thorny bark (71%, $n = 108$) or round-crowned trees with rough bark (18%). Conversely, nests on sand were found mainly in round-crowned trees with rough bark (79%, $n = 100$) or flat-topped trees with thorny bark (18%). This division reflects the abundance of nest trees on each biome (flat-topped thorn trees–basalt, round-crowned rough-barked trees–kalahari sand)

Mean internest distances between basalt ($\bar{x} = 4.74$ km, range=1.5–9.6 km, $n = 61$) and kalahari sand ($\bar{x} = 8.65$ km, range=3.4–18 km, $n = 45$) was significantly different ($z = 4.18$, Mann-Whitney U-test, $P < 0.01$).

LAYING TIME AND BREEDING SUCCESS

Most clutches ($n = 286$) were laid in May (43%) and June (51%). There was no significant difference in laying dates between biomes although a trend for later laying on sand was recorded ($\chi^2 = 5.74$, $P < 0.10$). Significantly more pairs laid in May during 1973 to 1976 when compared with 1979 to 1984 ($\chi^2 = 22.03$, $P < 0.01$) (Table 1).

There was no relationship between peak laying month and the number of chicks reared (basalt $r_s = 0.20$, sand $r_s = -0.05$, $n = 10$, both values $P > 0.05$). However, significantly more clutches were laid early between 1973 and 1976 (see above) and significantly more young were reared per breeding attempt ($\chi^2 = 10.75$, $P < 0.05$). This suggests that early laying may result in successful breeding, but the overall influence here is probably the differing amounts of rainfall during these periods.

CLUTCH SIZE AND BREEDING SUCCESS

Seventy three percent of all clutches seen ($n = 74$) were two-egg clutches. Significantly more two-egg clutches were recorded on basalt (82%, $n = 44$) when compared to sand (60%, $n = 30$, $\chi^2 = 4.32$, $P < 0.05$). Of 23 two-egg clutches with known breeding outcomes on basalt, 52% were successful compared to 60% of 15 two-egg clutches on the sand ($\chi^2 = 0.08$, $P > 0.05$). One-egg clutches on sand (30%, $n = 10$) had similar success to one-egg clutches on basalt (25%, $n = 4$). Significantly more one-egg clutches were recorded between 1979 and 1984 (90%, $n = 20$)

TABLE 1. Annual variation in monthly egg-laying dates (April to August) and breeding success (number of attempts) for African Hawk-Eagles nesting on basalt and kalahari sand in Hwange National Park. Annual rainfall in mm.

	Basalt							Kalahari sand							
						Breeding success							Breeding success		Rain
	April	May	June	July	August	%	*n*	April	May	June	July	August	%	*n*	(mm)
1973		2	10			100	(12)		5	5			100	(12)	430
1974		9	10			89	(19)		6	7			94	(16)	1,160
1975		16	3			78	(9)		8	1			83	(6)	850
1976		14	9			79	(33)		5	5			56	(16)	690
1979		2	2			27	(30)	1	3	8	3		40	(30)	620
1980		10	8	1	1	56	(39)	2	8	12	2		56	(34)	640
1981		2	19			61	(38)		6	13			59	(34)	940
1982		3	9	3		52	(31)		4	5	2		31	(26)	380
1983		6	3			57	(23)		4	4			53	(15)	585
1984		1	10	1		32	(22)		1	7	5		38	(16)	445

($\chi^2 = 36.42$, $P < 0.01$) with most being laid on kalahari sand.

No natural replacement clutches were recorded but two pairs relaid 11 and 13 days after their clutches had been collected early in incubation. Only one fledgling was observed in all cases, the first hatched usually killing the second within 10 days of hatching.

BREEDING SUCCESS AND BEST AREAS

From 256 breeding attempts on basalt, 151 chicks were reared giving a mean success of 0.59 chicks reared/pair/year. A significantly greater number of chicks/attempt (0.85) were reared from 1973 to 1976 (mean annual rainfall 785 mm) when compared with 1979 to 1984 (0.49 chicks/attempt; mean annual rainfall 601 mm; $\chi^2 = 8.15$, $P < 0.01$).

From 206 kalahari sand breeding attempts, 112 chicks were reared; a mean success of 0.54 chicks reared/pair/year. Significantly more chicks were reared/attempt in 1973 to 1976 (0.78) when compared with 1979 to 1984 (0.47 chicks/attempt; $\chi^2 = 5.22$, $P < 0.05$).

On basalt, mean number of breeding attempts decreased from west to east, with western pairs at Robins, Toms, and Deteema having significantly more attempts than the eastern pairs at Lukosi, Ecotone, and Inyantue ($z = 2.22$, $P < 0.05$, Table 2). There was also a tendency for western pairs to produce more chicks/attempt (0.66) than pairs in the east (0.53) but this difference is not significant ($z = 1.68$). Pairs in the northern part of the sand biome at Ecotone, Camp, Central, Triga, and Mitswiri attempted to breed significantly more often than the southerly pairs at Fossil, Teak, Pans, and Seeps ($z = 2.10$, $P < 0.05$), but the mean number of chicks produced was similar ($z = 1.13$).

DISCUSSION

Since raptor numbers are determined by food availability (Newton 1979) birds in less productive areas should be spaced further apart than in more productive areas. The lower primary production on the kalahari sand probably results in fewer consumers. Presumably the eagles have responded by having much larger internest dis-

TABLE 2. Breeding success of African Hawk-Eagles nesting in different geographical areas within basalt and kalahari sand biomes in Hwange National Park.

Location	Mean attempts/ known pair	Chicks reared/ pair/year	Attempts × chicks reared	*n*
		Basalt		
Toms	5.6	0.68	3.81	8
Robins	6.0	0.46	2.76	3
Deteema	4.4	0.68	2.99	9
Lukosi	3.9	0.57	2.22	26
Inyantue	3.4	0.58	2.26	8
Ecotone	3.3	0.60	1.98	3
South	4.5	0.68	3.06	6
		Kalahari sand		
Ecotone	4.2	0.48	2.02	16
Camp	3.7	0.50	1.85	9
Central	4.3	0.57	2.45	6
Triga	4.7	0.58	2.73	3
Mitswiri	6.3	0.43	2.71	3
Fossil	3.3	0.68	2.24	6
Teak	3.3	0.50	1.65	8
Seeps	3.0	0.67	2.01	1
Pans	1.0	0.00	0.00	1

tances and home ranges than pairs on the more productive basalts. However, the larger internest distances of kalahari sand pairs probably compensate for the lower number of prey animals, and they breed as successfully as the basalt pairs.

The significantly different internest spacing suggests that eagle densities may be limited by differing primary production on basalt and kalahari sand. Tarboton (1980) recorded much higher densities of five gamebird species on eutrophic clay soils than on distrophic sandy soils (densities for all five species combined; 82.6 vs. 36.7 birds/100 ha) in South Africa. The greater diversity and number of gamebird prey species on basalt (seven species) against kalahari sand (five species) (Hustler 1986) and the scarcity of bush squirrels on the sand (pers. observ.) suggests that these pairs have to work harder for prey which is scarcer and are spaced further apart as a result.

In years of poor rainfall on poor soil, it could be expected that productivity would be low. This would be reflected in all trophic levels. African Hawk-Eagles laid earlier and reared more chicks/breeding attempt between 1973 and 1976 than between 1979 and 1984. The trend towards later laying by sand pairs suggests a food stress in this area which causes adults to come into breeding condition later than birds on the more productive basalts. Furthermore, the high incidence of one-egg clutches between 1979 and 1984 on kalahari sand in particular suggests a great food stress created through a reduction in productivity resulting from below average rainfall. Similarly the lower number of chicks produced between 1979 and 1984 in both areas is probably also a function of reduced food at that time.

Pairs breeding in the more open western sector of the basalt area attempt to breed more often and produce more chicks than pairs in the eastern portion of the area. Likewise, on sand, pairs nesting in more open areas attempted to breed more often than pairs in the more heavily wooded areas in this biome. This suggests that parts of the park may be marginal habitat for the African Hawk-Eagle as the woodland in these areas is too well-developed.

Newton (1979) suggests that food and nest-site availability limit raptor breeding densities. In Hwange National Park, nest sites for African Hawk-Eagles are not limited. Food densities may be different as a result of unequal productivity on each biome. This is complicated by differing prey diversity which may require different hunting techniques and effort. However the lowered breeding success on both biomes during a period of reduced rainfall suggests that overall prey density and availability is important. The different breeding densities of African Hawk-Eagles in biomes with different primary production confirms Newton's (1979) postulate that food availability determines densities of eagles in the tropics.

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