Timing of breeding of the redbilled oxpecker (*Buphagus erythrorhynchus*) in the Kruger National Park

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The reproductive activity of the redbilled oxpecker *Buphagus erythrorhynchus* is governed primarily by the effects of rainfall and the onset of the laying cycle is dependent on the time of year at which the rain occurs. At the onset of the rainy season in August or early September the biomass of the Ixodidae increases on the mammalian symbionts and is made use of for feather synthesis during moult. During October with a significant increase in the biomass of Tabanidae it is possible to accumulate a large enough protein reserve to initiate breeding.

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Voortplanting in die rooibek-renostervoël *Buphagus erythrorhynchus* word hoofsaaklik deur die effek van reënval beheer terwyl die tyd wanneer die eerste eiers gelê word deur die reëntydinterval bepaal word. Aan die begin van die reënseisoen gedurende Augustus en begin September verhoog die biomassa van Ixodidae op die soogdiersimbionte wat vir die sintese van vere tydens ververing benodig word. Gedurende Oktober, met 'n betekenisvolle verhoging in die biomassa van die Tabanidae, is dit moontlik om 'n voldoende reserwe proteïne op te bou en te begin broei.

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In the Kruger National Park the redbilled oxpecker *Buphagus erythrorhynchus* breeds during the summer months, October to March, successfully raising up to three broods in a season. For the present purpose the breeding season is defined as those months in which eggs and chicks are found in any nest. Breeding occurs in natural cavities in trees with animal hair and dung predominantly used for nesting material (Stutterheim 1976). The reason why oxpeckers (Buphaginae) breed during the wet summer months is not known. Dowsett (1965) speculated that the best time to breed would be towards the end of the dry season when ungulates are in poor condition and are carrying a heavy tick load. At this time the herds are concentrated around water supplies and ticks would be readily accessible. In contrast, during the wet summer months ungulates are considerably dispersed and could be difficulut to see in the dense vegetation. By calculating the average monthly mass of the ovaries and testes of *B. erythrorhynchus* and comparing the data with known variables such as temperature, day length, rainfall and abundance of Ixodoidea and Tabanidae, some deductions on the relative importance of these variables in determining the timing of egg laying are possible.

Materials and Methods

For a period of 18 months, from July 1973 to December 1974, eight oxpeckers were shot every month within a radius of 10 km around Skukuza (25°01′S/31°03′E). Because of the absence of a visual method for sexing oxpeckers (Stutterheim 1977), the sexes of the oxpeckers shot each month were not equally distributed in all months of the study. After examining the collected birds for moult, the testes, left ovary and stomach were dissected out and fixed in 40% alcohol. Mass (to the nearest 0,0001 g) of testes and ovaries was determined in a sealed jar containing filter paper saturated with alcohol to minimize error through evaporation, as suggested by Mackie & Buechner (1963). The stomach contents were analysed and described by Bezuidenhout & Stutterheim (1980). Daily rainfall and maximum and minimum temperatures were recorded at the Skukuza weather station. Average monthly temperature was calculated from the average daily maximum and minimum temperatures and length of daylight from the formula suggested by P. Vorster (pers. comm. 1975):

Daylength	=	$12 \pm 12 \tan \phi \tan \alpha$
where ϕ	=	latitude of Skukuza
and α	=	declination of the sun on the specific date.

Ixodid ticks and blood-sucking flies form the major foods of *B. erythrorhynchus* (Moreau 1933; Bezuidenhout & Stutterheim 1980). An indication of seasonal variation in the biomass of Ixodidae was obtained monthly from October 1973 to December 1974 by culling an adult impala ram once a month in the vicinity of Skukuza, combing its hair with a steel comb and collecting all ticks. From January to December 1974 trends of the Tabanidae numbers were determined by erecting a Harris fly-trap for 24 h a month on the same site near Skukuza (Bezuidenhout & Stutterheim 1980).

Breeding behaviour was studied at 43 nests in the Satara area, 90 km north of Skukuza, over two breeding seasons, October to March in 1973/74 and October to January in 1974/75. It was assumed that breeding would be the same in the two areas. The study area was scouted every day and all nests found were examined every second day and where necessary every day, so that the phases of each nesting cycle could be determined to the nearest day.

Results

The measurements of environmental variables and resources compared with the mass of *B. erythrorhynchus* gonads are shown in Figure 1. The date of commencement of egg laying in the 1973/74 breeding season is calculated from a sighting of the first fledgling on 5 December 1973. In *B. erythrorhynchus* the average period, from the day the first egg was laid until the last nestling had fledged was 42 days. The first egg laid was therefore calculated as 24 October 1973. The last chick fledged on 14 April 1974 indicating the duration of the breeding season as 173 days. In the 1974/75 breeding season the first fledgling was observed on 27 December 1974. From this the first successful breeding attempt can be calculated as 16 November 1974 which is 22 days later than in the previous year (Stutterheim 1976).

The moult cycle of *B. erythrorhynchus* was described by Stutterheim (1980). Body moult starts at the beginning of the rainy season in late August or early September. Body moult is completed by or delayed with the onset of the breeding season in late October but an overlap between moult and breeding occurs in the rectrices, primaries and greater upper primary coverts. There appears to be a difference in the onset of primary moult in the 1973 and 1974 moulting seasons with an earlier start during the 1973 moulting season.

Analysis of the stomach contents cannot be used to calculate the total amount of food consumed by an oxpecker in a given day because the method of collection was not standardized and the birds were not all shot at the same time of the day. No quantitative information is therefore

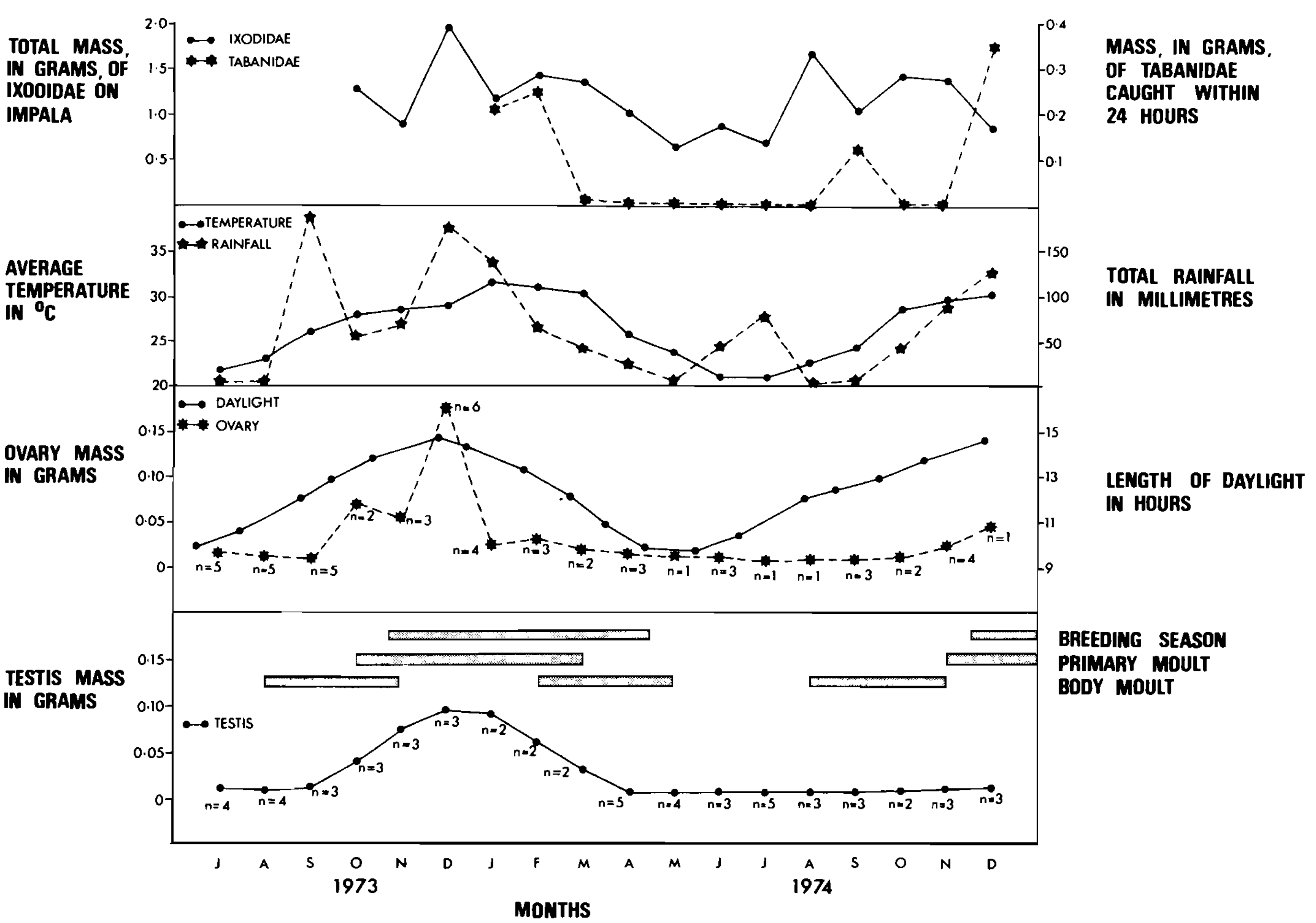

Figure 1 The mass of *B. erythrorhynchus* gonads and the environmental factors in the Skukuza area.

available on the number or biomass of ticks consumed during any particular season. The consumption of ticks, however, was not restricted to any particular season of the year as they were found in all the stomachs examined at various times during the year. Diptera were a source of food from August to April with a peak between November and March (Bezuidenhout & Stutterheim 1980). This corresponds to the pattern of Tabanidae caught in the Harris fly-trap (Figure 1).

A significant relationship (r = 0,96) was found between the monthly total tick counts from impala compared with rainfall and mean monthly temperature, i.e. the numbers of ticks on the mammalian symbionts increase during the summer months. The mean number of ticks found on impala ($\bar{x}$ = 502) during the summer months (September to March) was not significantly higher (t = 0,325; $P < 0{,}01$) than the mean number ($\bar{x}$ = 375) during the winter months (March to August). The reason for this is most probably the unseasonable 82 mm of rain in July 1974 which resulted in an increase in the number of ticks on impala. Their numbers, however, decreased again with only 2 mm of rain in August. Their numbers increased again from September and October ($\bar{x}$ = 469) but with a more significant increase (t = 40,2; $P > 0{,}01$) during November and December ($\bar{x}$ = 1044). The trapping results of the Harris fly-trap indicate that the number of Tabanidae increased after rainfall. This corresponds with the stomach contents analysis (Bezuidenhout & Stutterheim 1980) which indicated that flies were a source of food from August to April with a peak between November and March.

Discussion

Testis and ovary mass increased just before or during the period of onset of egg laying, 26 October in the 1973/74 breeding season and 16 November in the 1974/75 breeding season (Figure 1). The mean ovary mass in November 1974 at the onset of egg laying was lower ($\bar{x}$ = 0,03; n = 4) than that observed during October 1973 ($\bar{x}$ = 0,07; n = 3). The reason for this is that during the 1974/75 season nesting onset showed great variation with most nests starting during December (Stutterheim 1976). Not all the birds were therefore in breeding condition when collected on 11 November.

No correlation (r = 0,05) was found between the mean monthly temperature and the mass of the ovaries and testes. This accords with the view of Immelman (1970) who proposed that because of the irregularity and short-term fluctuations, temperature probably has no importance as a direct proximal factor to stimulate breeding. This was also emphasized by Kemp (1973) who found that breeding in *Tockus* was started during unseasonal cold weather. The mass of *Buphagus* gonads also does not increase as summer temperatures start to rise during August.

No correlation (r = −0,11) was found between the mass of the gonads and length of daylight. However, the data presented do not exclude the possibility that changing daylength may be the factor which triggers the new breeding season. Reiter & Follett (1980) indicated that a time lag between the perception of such a stimulus and an increase in gonad mass could occur. A time lag could therefore be the principal reason for the lack of correlation in the data in this regard.

Immelman (1970) speculated that factors such as the sudden availability of suitable nesting-material and camouflage for nest sites may also be responsible for proximal control of gonad development and reproductive behaviour. *B. erythrorhynchus* utilizes animal hair and dung as nesting material and utilizes natural cavities for breeding. The feeding habits of oxpeckers give rise to their dependence on their mammalian symbionts resulting in the year round availability of nesting material. Furthermore, natural cavities are also not related to any seasonal change in the environment.

No increase in the mass of the gonads was recorded before the first rains of each season. During the 1973/74 breeding season 187 mm of rain fell in September 1973 with egg laying taking place in October. During the 1974/75 breeding season 82 mm fell in July, 2 mm in August and 13 mm in September. Thereafter the rainfall increased steadily and the birds started breeding in November. It therefore appears that reproductive activity may be governed primarily by the effects of rainfall and that the onset of breeding is dependent on the time of year at which the rain occurs.

In the 1974/75 season the beginning of the rainy season followed the predicted pattern but subsequent rain fell in small but frequent showers. Variation in the onset of egg laying was great with most nests starting during the heavier rains of December 1974. *Buphagus* is a multiple brooded species and is able to raise up to three broods in a season (Stutterheim 1976). Thus if any birds started egg laying during December 1974 they only had time for two breeding sessions during the 1974/75 breeding season compared with three breeding sessions during the 1973/74 breeding season. This is probably the reason for the lower reproductive success (0,5 fledgling per adult) during the 1974/75 breeding season compared with 0,8 fledgling per adult in 1973/74 (Stutterheim 1976).

A secondary effect of rain that could be important in the case of oxpeckers is the dispersal of their mammalian symbionts. During the dry season, the symbionts are concentrated around the more permanent drinking places. It could be argued that if *Buphagus* bred in the dry season, they could very easily have found their symbionts around the available surface water. Because of the scarcity of suitable nesting holes and probably the defence of an area around the nesting locality, not all the birds could be able to breed in the vicinity of these permanent drinking places. Moreover, if such a water point dried up, it would be fatal for the chicks in the nests in the immediate vicinity of the water point as the game would move out of the area. The wet summer months are therefore the best time to breed. With the onset of the wet season the game disperse to more favoured grazing areas. With more surface water available, the daily foraging radius of the game decreases (Young 1970). With a smaller foraging radius it would thus be easier to find these mammals from the nest during the wet season.

According to Immelman (1970) the most important ultimate or evolutionary factor determining the timing of the breeding season for almost all species of birds is the availability of an adequate food-supply. Jones & Ward (1976) and Fogden & Fogden (1979) proposed that the proximal control of breeding in *Quelea quelea* and *Cama-*

roptera brevicaudata is provided by the individual's own body condition and particularly the state of its protein reserves. No environmental releasers are required for the birds to breed at the appropriate time of year. In the case of *B. erythrorhynchus* food supply could influence the individual's body condition. During the dry season the birds feed on Ixodidae which provides sufficient energy to supply normal maintenance. At the onset of the rainy season in late August or early September due to an increase in ambient temperature, and possibly, length of daylight, the biomass of the Ixodidae increases on the mammalian symbionts. The increase in the food supply is probably needed for the extra demand of feather synthesis during moult so a protein reserve is not accumulated and the birds do not breed. During October, with a significant increase in the biomass of Tabanidae, a completion or delay in body moult and a longer period of daylight which could provide a longer feeding period, it is possible to accumulate a large enough protein reserve to initiate breeding.

During the 1974/75 season, the rain in July 1974 was inadequate to stimulate a large enough food supply and the birds did not breed. The decline in precipitation during September and October resulted in a decrease in the food supply and only during November, when 90 mm of rain fell, did the Tabanidae become plentiful. This resulted in the birds accumulating sufficient protein to initiate egg production and laying.

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