THE BIOLOGY OF THE RED-BILLED OXPECKER, *BUPHAGUS ERYTHRORHYNCHUS* (STANLEY, 1814), IN THE KRUGER NATIONAL PARK

by

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Submitted in partial fulfillment of the
requirements for the degree of
M.Sc. (Zoology)

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ABSTRACT

The biology of the red-billed oxpecker, <u>Buphagus erythrorhynchus</u> (Stanley, 1814) in the Kruger National Park

by

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The behaviour, movements, moult cycle, breeding biology and ectoparasites of the red-billed oxpecker were studied in the Kruger National Park in the period March 1973 to December 1974. The oxpecker is adapted for a complicated and intimate relationship with certain large mammal species. A study population at Skukuza showed little or no fluctuations in numbers and no local movements. Primaries of the oxpecker had a sharply defined moulting season which extends over an 11 month period, whereas the secondary moult extends over a seven month period. Up to five birds regularly attend a given nest and all the members of a group feed the nestlings, guard them and later care for the fledglings. Only one female and one male participate in incubation. Mites, ticks, lice and louse flies were found to be ectoparasites of the oxpecker.

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CHAPTER 1

GENERAL INTRODUCTION

The oxpeckers of Africa, commonly known as tickbirds, are highly adapted to their peculiarly intimate and complicated relationship with certain large mammals. The name "Oxpecker" would appear to be derived from their habit of climbing over large mammals in order to obtain their food (Attwell 1966).

Oxpeckers are confined entirely to Africa south of the Sahara. There are two species, *Buphagus africanus* (Linnaeus), the yellow-billed oxpecker and *B. erythrorhynchus* (Stanley) the red-billed oxpecker. Although the range of the two species is vast, the fact that they are wholly dependent for a living on the presence of large domestic or wildlife ungulates means that their distribution is often very patchy. In broad terms, *B. africanus* occupies much of the country west of the Rift Valley system, crossing it only in the area immediately to the north of Mount Kenya and in western Tanzania; it is absent from areas of dense forest, though penetrating most of the more open parts of the Congo, and also from the southern tip of the continent. In effect, therefore, it occurs sporadically in a huge belt of country from Senegal to south-west Ethiopia and thence south to Natal. *B. erythrorhynchus* ranges south of the Sahara from Eritrea, Ethiopia and the south-east Sudan to Rhodesia and the Transvaal and Natal in South Africa. It is an eastern species, its westernly limit being approximately longitude 30° east (Pitman 1956).

In the last few decades, however, with the extension of dipping practices to kill ticks in most European stock farming areas, the numbers and distribution of oxpeckers have been greatly reduced. Their present day distribution is largely confined to game reserves and private game farms. On this account alone the importance of wildlife sanctuaries for the conservation of oxpeckers is indicated. Little is known about the ecology of the Buphaginae (Attwell 1966).

Knowledge of the general biology of any species is essential for conservation of that species. An investigation into the general ecology of the oxpecker was thus indicated and a study was undertaken in the Kruger National Park from March 1973 until December 1974. For some unknown reason *B. africanus* does not occur in the Kruger National Park. This study was thus confined to *B. erythrorhynchus*, although some reference is made to *B. africanus*. This study was an attempt to enlarge what is known about *B. erythrorhynchus* in South Africa, and it also collates some of the existing general knowledge for the two species from the rest of Africa.

CHAPTER 2

GENERAL MATERIALS AND METHODS

Dimensions

Measurements

All the oxpeckers trapped and collected in the Skukuza area were measured by using the methods advocated by Ledger (1969) and Pettingill (1970). The measurements of wing (flattened), wing-span, total length and tail are believed to be accurate to ± 1 mm and the measurements of the culmen and tarsometatarsus to the nearest 0,1 mm. Two age classes were used - adult birds (birds older than eight months) and immature birds (free flying birds younger than eight months) (see section under breeding behaviour). Because of a failure to sex live-trapped birds, the measurements of the adults were also divided into two classes - the measurements of all the adult birds, regardless of sex (trapped and collected birds), and measurements of adult males and females (only collected birds).

Mass

The data on the mass of the red-billed oxpecker were obtained during the course of ringing and collecting operations in the Skukuza area during the period March 1973 to December 1974. All weighings were made on a 100g capacity spring-balance and readings were taken to the nearest 1,0g. The time lapse between the birds being caught or collected and weighed was a matter of minutes. Trapped birds were weighed in cloth bags, the bags being weighed before and after processing each individual bird. Two age classes were used - adult birds (birds older than eight months) and immature birds (free flying birds younger than eight months) (see section under breeding behaviour). Because of a failure to sex live-trapped birds, the mass of the adults were also divided into two classes - the mass of all the adult birds regardless of sex (trapped and collected birds) and the mass of adult males and females (only collected birds). Sex was determined by dissection of the collected birds. A total of 342 birds were weighed.

General behaviour

In the study on the red-billed oxpecker, observations were made from a vehicle using 7 x 50 binoculars. Activities of the birds were timed with a stopwatch and the ambient temperature was measured with a Sekunden thermometer. Two methods were tried in an attempt to determine the daily activity pattern as suggested by Siegfried (pers. comm.).* As it was impossible to follow an individual bird continuously from dawn to dusk, an attempt was made to follow a group of mammals and their attendant oxpeckers. This was tried at three localities:

a) A hide was erected at the animal pens of the Veterinary Division near Skukuza. Because of human disturbances, no birds were present for long periods of the day and this attempt was abandoned.

b) An attempt was made to follow a group of white rhinoceros (_Diceros simus_) in a camp near Pretoriuskop. It was impossible to follow these animals continuously close enough to observe them without disturbing the birds and this attempt was also abandoned.

c) A breeding herd of roan antelope (_Hippotragus equinus_) was followed with a vehicle at Nwashitsumbe (Fig. 1). By selecting several activities that are easily recognised in the field, the activities of both the roan and birds were recorded every five minutes for the full-daylight period. The ambient temperature was recorded every hour by using a Sekunden thermometer. This was only done once during October so that no account can be given of a seasonal variation in activity. A disadvantage of this method was that the birds were constantly coming and going, with the result that this method describes only the behaviour of the birds on the roan antelope.

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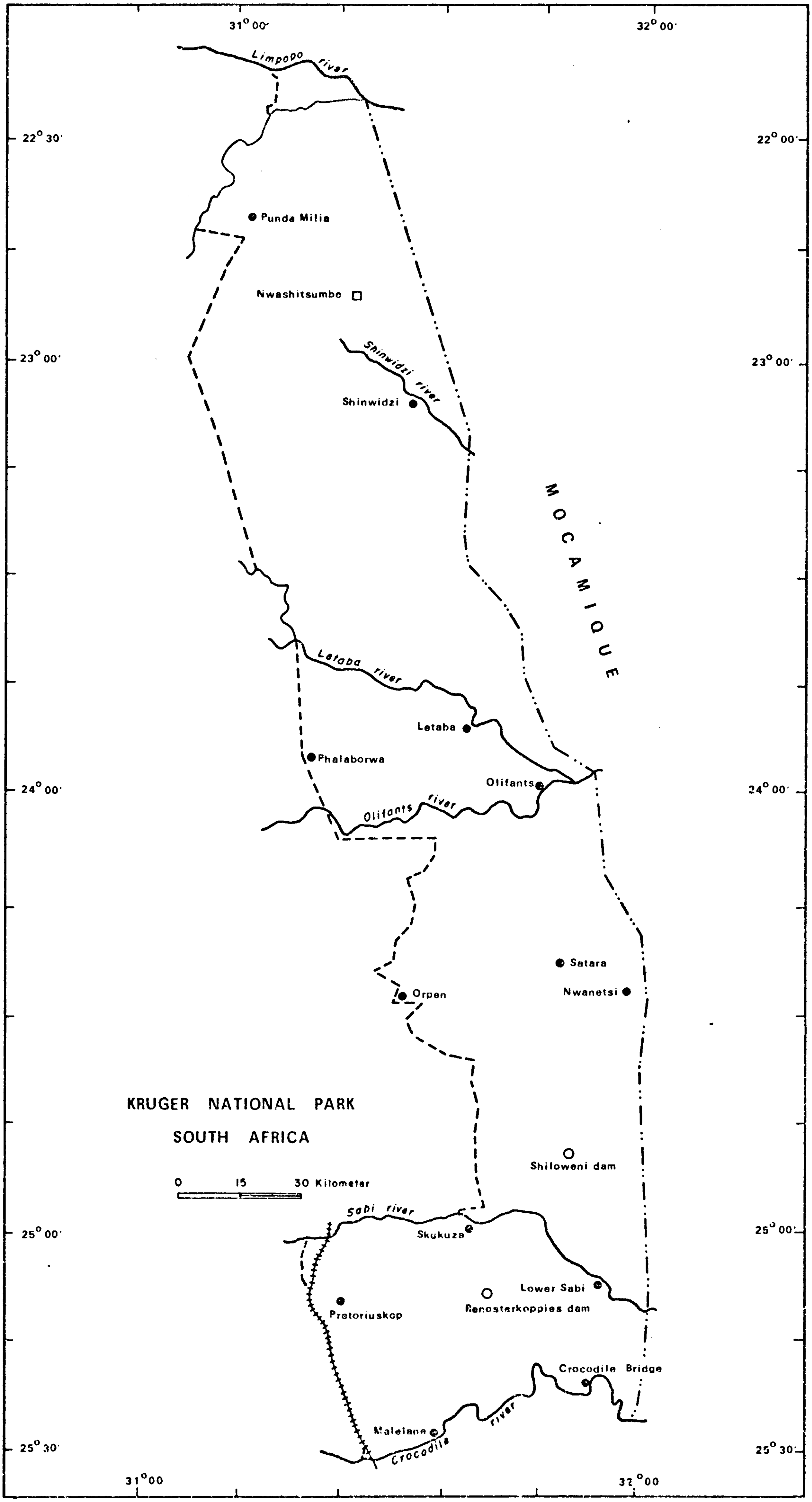

Fig. 1. A simplified map of the Kruger National Park with localities mentioned in the text

In the second method, data sheets were compiled for 12 mammalian species as advocated by Altmann (1974). Every time an oxpecker was sighted, the activity of the birds and mammals, time of day, ambient temperature and the date were recorded. By using this instantaneous and scan sampling method, a total of 1944 activities were recorded from July 1973 until December 1974. No activity recordings were made if the birds or mammals were disturbed by the presence of the observation vehicle. These activity data of the birds and mammals were then treated as if they had been obtained in one day. However, this method is not entirely satisfactory because the data were collected in all the seasons of the year and no adjustment is made for the change in the duirnal period. In this activity study five different activity states were used i.e. resting, feeding, sun bathing, comfort movements and feeding of young. Feeding includes all the activities associated with the search for food, plus the activities for consumption, once it was found. As it was not always possible to see whether a bird was sitting, perching or thermoregulating, these three activities were combined in the analysis under resting. Comfort movements include preening, bill-wiping and head-scratching.

Movements

Trapping

The red-billed oxpecker spend most of their activity period on the mammalian symbiont and they are therefore not easy to trap (Stutterheim 1974). The word mammalian symbiont is used because a symbiotic relationship exists between the oxpecker and its mammalian associates, for the birds warn the mammal of impending danger, and relieve them of ectoparasites, flies and probably wound-parasites in return for food supplies (Attwell 1966). The mammal associates could be referred to as hosts, although in a strict zoological sense they do not fill such a role. The mammal associates are in fact true hosts to their ectoparasites, the ticks and the biting flies, which constitute the main food supply of the birds. The use of a baited net fitted with nooses on a donkey (Davidson 1963) is recommended in the literature but was not found practical in the Kruger National Park. Van Someren (1951) observed the peculiar behaviour of oxpeckers sitting and flying down hollow structures and suggested using a stove chimney for trapping purposes. This method was tried by Bezuidenhout (pers. comm.)* but without any success. Oxpeckers were observed sitting on a metal chimney near Skukuza but never flew down the chimney. This chimney was probably used as an observation post because it is much higher than the surrounding trees.

Large numbers of oxpeckers are attracted by their mammalian symbionts kept in open pens. At the animal holding pens of the Veterinary Division near Skukuza, oxpeckers are attracted by buffalo, wildebeest and cattle kept in three adjacent pens. By erecting two 20 m x 2,6 m x 36 mm terelyne mist nets in these camps a total of 155 oxpeckers were caught with 48 recaptures in a period of 19 months (Plate 1). The birds were caught while flying from one group of animals to animals in an adjacent pen. Very few birds were caught while settling on the animals or flying away. The reason for this is the birds' steep angle of ascent and descent. Because of behavioural studies on the oxpeckers at these pens, the birds were trapped only once a month to reduce disturbance to a minimum. This trapping method proved to be quite successful but not entirely satisfactory due to the following factors:

a) The nets had no camouflaging background and the birds easily avoided them.

b) No birds were caught during the feeding times of the mammals due to disturbances by humans.

c) After the first trapping session the birds became "net shy". This is clearly illustrated in the first full-day trapping success of 24 birds and mean trapping success of 7,5 birds per day.

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Plate 1. An adult oxpecker entangled in a mist net at Skukuza, December 1974.

Plate 2. The marking methods tried on the red-billed oxpecker at Skukuza: 1. Coloured neckband. 2. Backtag marker. 3. Poncho marker. 4. Colour rings. 5. Wing tag.

Plate 3. A red-billed oxpecker marked by means of colour ringing, December 1974.

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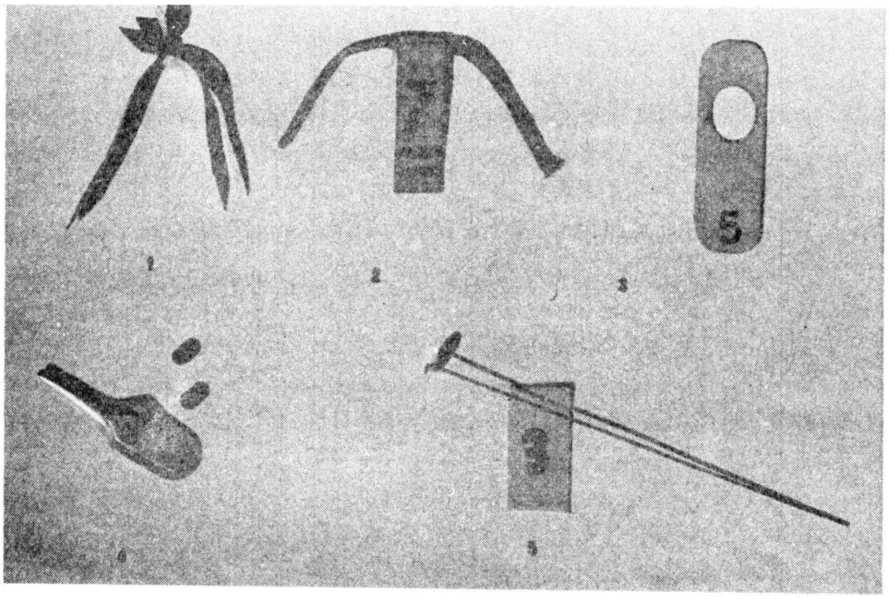

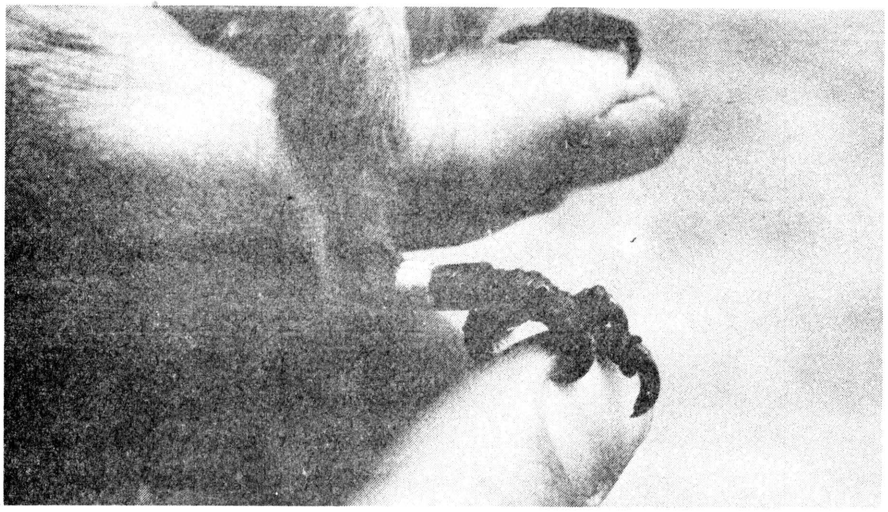

d) A large number of laughing doves' (*Streptopelia senegalensis*), cape starlings (*Lamprotornis nitens*), pin-tailed whydas (*Vidua macroura*) and grey-headed sparrows (*Passer griseus*) visited the pens and often flew into the nets. These birds had to be removed with the result that oxpeckers on the animals were disturbed. Every hour all oxpeckers caught in nets had to be removed and this also resulted in disturbing all the birds present.

e) During March 1974, a little sparrow-hawk (*Accipiter minnullus*) used the animal holding pens as a hunting area. The presence of this raptor reduced the trapping success to 3,5 birds per day.

f) A large number of nets were damaged by buffalo in the pens. This problem was solved by wiring the net-poles to the fence.

This trapping method appeared to be quite safe for no mortality occurred and no visible external injuries were observed.

Colour marking

Marking birds to enable field identification of individuals without rehandling is important in most wildlife research projects. Preferred marking techniques are those which have the least effect upon the behaviour and survival of the marked birds (Gullion *et al.* 1962).

colour neckbands

Neckbands were used with success on Canada geese (*Branta canadensis*) (Craighead and Stockstad 1956) and on the crested barbet (*Trachyphonus voullanttii*) (Nel pers. comm.)*. The material used for neckbands is a fluorescent, plastic-coated nylon fabric with the trade mark "Saflag". The neckbands were made from 2 cm "Saflag" strips and after punching two holes into a strip it was tied around the neck of the bird

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by means of a jesse knot (Plate 2). "Saflag" is only available in six colours but by two-colour combinations, a large number of different colour combinations are possible.

Identification of the neckband depends on the streamers formed at the connection between the two different coloured strips, because the birds preened the neckbands into their feathers. These neckbands were visible from a distance of about 100 m. The oxpeckers frequently nibbled at the streamers and after eight months they were completely worn down and in most cases impossible to identify. This was probably due to the sharp cutting edges of the bill. Too tightly fitted neckbandsformed abrasions and too loosely fitted neckbands got entangled with the bill. Colour fading was apparent after about four months.

Only 26 birds were marked by this method, which was abandoned because two birds were observed pulling the marker to such a position that they could not disengage their beaks, and they became embridled in the neckband. Bridling in the wild would be fatal. Birds, however, marked with colour neckbands were seen feeding their young and a neckband-marked bird was retrapped after a period of 17 months. It would appear, therefore, that properly fitted neckbands had no harmful effect on the birds.

poncho markers

Poncho markers were used with success on sage grouse (Centrocercus urophasianus) by Pyrah (1970). A poncho marker with smaller dimensions was made from 2,5 cm white "Saflag" strips with a circular hole in the centre (Plate 2). Numbers were painted with a quick-drying airplane dope on the poncho marker. These numbers were easily visible from a distance of 100 m. The hole in the centre of the poncho is slipped over the bird's head and the poncho is worked down the neck and under the lower feathers which hold the marker in place. Only two birds were marked by this method. Both birds became bridled by the poncho marker and were found dead the following day.

backtag markers

Labisky and Mann (1962) devised a backtag marker for ring-necked pheasants (Phasianus colchicus). A lighter and modified backtag with a serial number was made of "Saflag" and thin nylon string and tested on Cape sparrows (Passer melanurus) (Plate 2). It was found to hamper their flying and the method was abandoned (Stutterheim 1974).

ring tags

By following the design used by Murton et al. (1971) wing tags were made from stainless steel dental wire, nylon washers and a "Saflag" number tag (Plate 2). Captive birds were able to reach these tags and nibbled them. Because of possible injuries to the birds it was decided not to use this method.

colour rings

Colour ringing is one of the simplest and most widespread of methods for individual recognition. Three-millimeter split ring colour rings supplied by the National Unit for Bird-ringing Administration were used. Standard 4,3 mm incoloy rings were used in combination with the colour rings to avoid loss of identity through losing one or more colour rings. Although oxpeckers have a short tarsus, these colour rings could be identified at a distance of about 50 m with a pair of 7 x 50 binoculars (Plate 3). The advantage of this method is that it is very safe and has no visible disturbing effect on the oxpeckers. With nine different colours available, a vast number of colour combinations was possible. These rings are suitable in moderate climatic conditions, but after a short period of about 4 months of use, colour fading was already apparent. A total of 120 oxpeckers were marked by this method and after a period of 19 months no loss of rings or evidence of leg mutilation was found.

Age and sex of live-trapped birds

Three unsuccessful methods were tried in an attempt to sex live-trapped birds. The methods tried were cloacal examination, laparotomy and an analysis of the dimensions of the birds. Because of this failure to sex the birds, only two classes were used - adult birds (birds older than eight months) and immature birds (free flying birds younger than eight months) (see section under breeding behaviour).

Locating marked birds

The birds marked at Skukuza were located by using a vehicle driven along regular routes and identified with 7 x 50 binoculars. The sightings of marked birds were plotted on a large scale map.

The moult cycle

Moult was examined on 348 specimens of the red-billed oxpecker. These specimens consisted of 206 birds live-trapped monthly at Skukuza between March 1973 - December 1974 and 142 birds collected monthly in the Skukuza area between July 1973 - December 1974. The feathers were carefully examined in good light for colour and wear, and the progress of the moult was scored by using the methods of Humphrey and Parks (1959), Ashmole (1962), Evans (1966), Ledger (1969) and Siegfried (1971a).

As it was impossible to age a bird after about eight months, only two age classes were used: first-year birds, and those older than one year (adult birds) (see section under the post-fledgling period). When the actual field observations were made, each remex and rectrix was recorded as being either old, growing (at various stages) or new. For the remiges and rectrices a zero score was allocated to an old feather, one to a feather in pin or missing as a result of moult; two, three and four to feathers up to one-quarter, half or three-quarters growth respectively, and five to a full-grown new feather. The separate scores for the primaries, secondaries and tertials gave a total score of 50, 30 and 15 respectively. As indicated by Ashmole (1962) this system presumes that each feather takes about equal time to go through each of the four stages denoted by the numbers 1 to 4. There is no difference between a maximum and minimum moult score, the former eventually becoming the latter. However, since there is a considerable span of time between the end of a moult cycle and the beginning of the next one, this does not raise any difficulties. From these moult scores mean values were calculated for each month and the progression of moult expressed quantitatively.

For body moult the body was divided into 14 regions and if more than five feathers in a region were found to be moulting, that specific region was described as in moult. Although this method was not very accurate, it can be used for describing the main trends of body moult. As it was impossible to sex live-trapped birds, sexes were not distinguished in this study.

Breeding biology

The breeding biology was studied over two summer breeding seasons in 1973/74 and 1974/75, with a return visit in June 1975 for a reproductive success count and to extend some long term observations.

A total of 43 nests were found. After the breeding season notes were taken on the dimensions of the nest cavity and nest entrance, habitat surrounding the nest, nest and tree height and the nesting-material collected. A quantitative study of the nesting-material was made after dividing it into different components.

The nests were examined every second day and where necessary, once every day, so that the phases of the nesting cycle are only known to the nearest day. Nest contents were examined by using a dentist's mirror, while lighting the nest cavity with a torch bulb connected to a battery. A total of 364 h of observation, consisting of 26 full light-hour observations, were carried out at the nests. Observations were made from a vehicle parked about 50 m from the nest. The behaviour of the adult birds was timed with a stopwatch and the ambient temperature measured every half hour with a Sekunden thermometer in the shade about two metres above ground level.

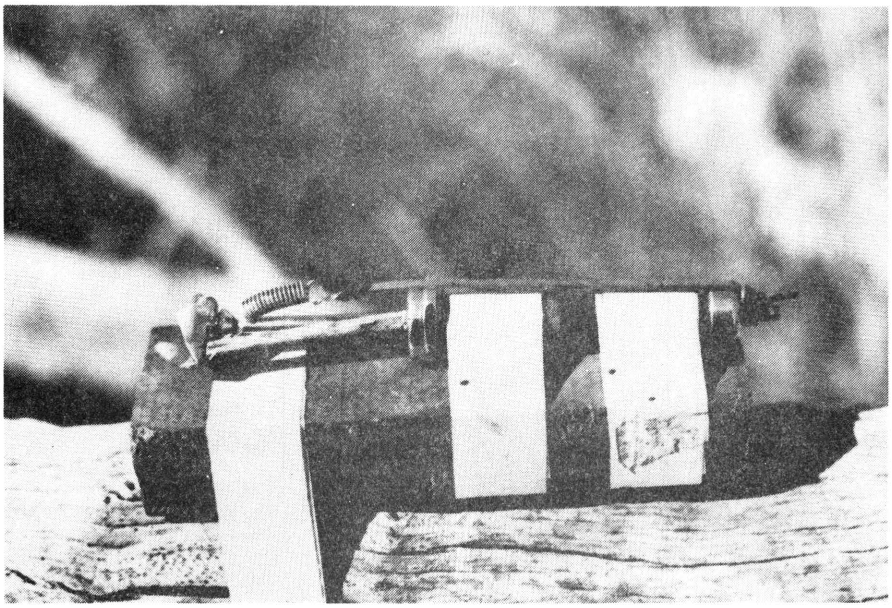
Post-natal development studies were carried out on chicks at eight nests. The chicks were weighed, measured and described every second day during the nestling period. They were also colour marked by using standard 4,3 mm incoloy rings in combination with colour rings for identification purposes, behaviour and movement studies. Two chicks were removed from the nests and hand-raised for development and behaviour studies. These chicks were fed on a mixture of "Pro Nutro", egg yolk and minced meat.

The red-billed oxpecker shows no visible sex or age differentiation in birds older than about eight months. Studies of marked adult and juvenile birds were, therefore, essential for the elucidation of the breeding behaviour. At three nests the adult birds were colour marked for an intensive social behaviour study. At two nests the adult birds were caught by erecting a mist net in front of the nesting hole. These birds were colour marked with colour rings and spot marked with a quick drying "aeroplane dope". At the third nest the adult birds were sprayed with Nyanzol A by using a syringe fitted with a spring around the plunger (Plate 4). A trigger mechanism was fitted to the plunger so that the syringe could be manipulated from a distance. As it was impossible to sex adult birds in the hand, the birds were collected after the observation period and were examined internally by dissection.

An intensive study area of 16 ha was established in the Satara experimental plots (Fig. 1). The area was regularly travelled and the locations of all nests within the area were recorded. To determine the dominant tree species and to check the preference of oxpeckers for certain tree species in the study area, a count was made of the trees large enough to contain an oxpecker nest and the occurrence of large enough breeding holes.

All instances of predation or other causes of natural death were recorded. If predation was recorded at a nest, live-traps were used in an attempt to determine the species

Plate 4. Syringe used for colour marking oxpeckers at the nest during the breeding season, December 1974.



of predator involved. The nests were also frequently visited at night.

Ectoparasites

By using the methods of Watson and Amerson (1967) a total of 68 ectoparasite samples were collected from oxpeckers in the Skukuza and Satara areas.

CHAPTER 3

STUDY AREA

Geographical location and topography

The Kruger National Park, which encompasses an area of some 1901119 ha is bordered on its north and south by the Limpopo and Crocodile rivers respectively (Fig. 1). The eastern boundary is formed to a large extent by the Lebombo mountain range, while on the west the boudary is formed by some 480 km of barbed-wire fence (Smuts 1972).

The Park, which lies between the Drakensberg escarpment and the Indian ocean (between latitude 25,25 S to 25,32 E and longitude 30,50 S and 32,2 E), is drained by two major river systems - the Limpopo and the Incomati (Pienaar 1968). Each of these major systems are fed by a number of sub-systems (primarily perennial) which are in turn fed by several important seasonal tributaries. The Limpopo river and its sub-systems, as well as those of the Incomati, pass through the Park in a west-east direction. The seasonal rivers usually only flow for a short time during the rainy summer months, but form important drinking sites due to a series of semi-permanent pools along their length (Smuts 1972).

Topographically the Kruger National Park is rather interesting, since, although appearing rather flat, it in fact presents an undulating landscape interrupted at intervals by deep seasonal or perennial water courses and rocky outcrops or koppies. There are no true mountain ranges in the Park, but the Lebombo ridges on the eastern boundary, the Malelane area and the area north of Punda Milia may be described as mountainous (Pienaar 1963). Just west of the Lebombo ridge the country tends to be rather flat, in contrast to the western half of the Park, and is consequently known as the Lebombo flats. The highest altitudes are attained in the south-west (835 m above sea level). Towards the east there is a gradual decline, with the Lebombo flats only some 180 - 240 m above sea level (Smuts 1972).

Climate

In the Kruger National Park rainfall occurs primarily as thundershowers which may occasionally be accompanied by lightning and hail. More than 80% of the rain falls during the summer months (October to March); almost rainless periods of up to three months are common. The mean annual rainfall varies from about 390 mm in the extreme north-east at Pafuri to 706 mm in the south-west at Pretoriuskop. There is thus an increase in the mean annual precipitation from north to south (Smuts 1972).

Temperatures may vary between 0° C to over 40° C (Young 1970). Abnormally low temperatures of -4,2° C were measured during the winter of 1964 (Van Wyk 1971 In: Smuts 1972). November and December are generally the hottest months, while June and July are the coldest with frost sometimes occurring in low-lying areas on cloudless nights. Relative percentage humidity may vary between 100% and less than 10% (Young 1970).

Habitats

Adequate descriptions of the vegetation and classification of the vegetation types of the study area have been provided by Van der Schijff (1957 and 1958), Pienaar (1963) and Brynard (1964, In: Smuts 1972). Van Wyk (1972) gives the most recent and up to date classification of the vegetation types of the study area as follows:

1. _Diplorrhynohus condylocarpon_/_Burkea africana_ woodland.
2. Climax _Colophospermum mopane_ forest.
3. _Colophospermum mopane_/_Combretum apiculatum_ woodland.
4. _Colophospermum mopane_ shrub savanna.
5. _Baphia massalensis_/_Guibourtia conjugata_ shrub with scattered trees.
6. _Colophospermum mopane_/_Combretum apiculatum_ woodland of the Lebombo range.
7. _Combretum apiculatum_/_Acacia nigrescens_ woodland.
8. _Acacia nigrescens_ /_Sclerocarya caffra_ woodland savanna.
9. _Combretum apiculatum_/_Acacia_/_Pterocarpus rotundifolius_ woodland of the Lebombo range.
10. _Pseudolachnostylis maprouneifolia_/_Strychnos_ woodland (Pumbe Sandveld).

11. *Acacia welwitschii*/*Albizia evansii* thorn forest.
12. *Acacia*/*Combretum* open woodland with closed lower layers.
13. *Combretum* woodland of the Malelane hills.
14. *Terminalia sericea*/*Dichrostachys cinerea* savanna woodland with tall grass.
15. *Acacia nigrescens* /*Albizia harveyi* woodland savanna.

Large mammals

The numerical status of the larger herbivorous species as determined by an aerial and ground census conducted in August 1973 (Joubert 1973) is given in Table 1.

Table 1 : Numerical status of the larger herbivorous mammals in the Kruger National Park (August, 1973).*

Species	Total number in Kruger National Park
Impala (*Aepyceros melampus*)	154100
Buffalo (*Syncerus caffer*)	22014
Zebra (*Equus burchelli*)	16500
Wildebeest (*Connochaetus taurinus*)	10100
Elephant (*Loxodonta africana*)	7965
Kudu (*Tragelaphus strepsiceros*)	7200
Giraffe (*Giraffa camelopardalis*)	4125
Waterbuck (*Kobus ellipsiprymnus*)	3100
Warthog (*Phacochoerus aethiopicus*)	2695
Sable Antelope (*Hippotragus niger*)	1211
Nyala (*Nyala angasi*)	745
Tsessebe (*Damaliscus lunatus*)	635
Eland (*Taurotragus oryx*)	340
Roan Antelope (*Hippotragus equinus*)	333
Hippopotamus (*Hippopotamus amphibius*)	2310
White Rhinoceros (*Diceros simus*)	186

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* As given by Joubert (1973)

CHAPTER 4

THE BIRD

Systematic position

The two species of African oxpeckers are classified by some systematists with the starlings (family Sturnidae) (Lowe 1938; Amadon 1943). In general, starlings may be described as Old World song-birds of medium or tending towards large, average size, with fairly long, usually slightly arched bills, the nostrils exposed, legs and feet fairly strong and in most species with a glossy green or bluish coloration. They lay greenish blue eggs, usually spotted, but sometimes immaculate, in nests in holes and in a few cases constructing clumsy nests of masses of sticks. The oxpeckers, however, are so aberrant that McLachlan and Liversidge (1970) have questioned their inclusion in the family Sturnidae and placed them under the family Buphagidae. According to Amadon (1956), however, the consensus is that they are starlings and their peculiarities are to be attributed to the divergence which follows when a species acquires markedly different habits from its relatives. In the oxpecker, the bill is very peculiar (for collecting ticks from mammals), there is no gloss in the plumage, the legs are small, the claws curved and sharp, and the tail pointed. Characters of the Sturnidae which have been retained are the wing structure and other morphological resemblances, the harsh unpleasant calls, and the habit of nesting in holes of trees. There is a certain degree of resemblance to Scissirostum (a starling species of Celebes), but this is presumably secondary. In Scissirostum the strong beak is used to dig nesting holes, woodpecker fashion, in dead wood, while in the oxpecker the bill is used to collect ticks from mammals. Lowe (1938) found that the oxpecker is in all respects a starling in the wide sense, but that it differs so much in respect of the morphology of its maxillo-palatines and vomer as to suggest its distinction by subfamily rank in the Buphaginae.

Plumage and colours

The general upper surface colour of the adult red-billed oxpecker is uniformly hair brown with a slight olive overlay with the head region the same colour as the upper-parts. On the underside, the throat and upper breast are hair-brown, grading into a cream-buff over the rest of the under-parts. The axillaries and underwing coverts are blackish with the wing coverts and secondaries a dark hair-brown. The bastard wing, primary coverts and primaries are also blackish but the latter has a paler, more vinaceous tinged inner-web. The tail is dark hair-brown. According to Attwell (1966) the plumage has a hairlike texture which fits closely and does not easily blow about and as Pitman (1956) indicates, this is an advantage when the birds spend most of their time on the exposed bodies of their mammalian symbionts. The beak is bright waxy-red, the tongue and the interior of the mouth are scarlet; the iris yellow to red, and the eyes rimmed with a narrow ring of chrome-yellow bare skin. Legs and toes are a dark brown.

Dimensions

Measurements

The measurements for adult and immatures are presented in Tables 2, 3, 4 and 5. Measurements of different parts of the body in McLachlan and Liversidge (1970) are smaller compared to the measurements of the birds from Skukuza, except in the case of the female's wing-length. This is probably due to the small sample (n = 10) given in McLachlan and Liversidge (1970).

The frequency distribution of measurements of all adult birds was plotted in quest of any discernable sexual dimorphism. In all the parameters, no deviation from the normal distribution was apparent (Fig. 2). When these measurements were further analysed, however, a statistically significant size difference (t-test, $P < 0,05$) in wing-length, wing-span and length of tail were found between males and females, with the males having a longer tail and wing. However, with

Table 2 : Measurements of adult* female red-billed oxpeckers collected in the Skukuza area during March 1973 - December 1974.

Dimensions	Number measured	Mean ± SE mm	Range mm
Wing	55	115,83 ± 0,45	107-121
Tarsometatarsus	55	22,10 ± 0,29	20,5-26,6
Culmen	55	17,22 ± 0,11	15,8-18,6
Wing-span	51	344,67 ± 1,20	340-380
Tail	53	94,57 ± 0,49	84-103
Total length	48	222,94 ± 1,13	212-259

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* Birds older than eight months (see section under breeding behaviour).

Table 3 : Measurements of adult* male red-billed oxpeckers collected in the Skukuza area during March 1973 - December 1974

Dimensions	Number measured	Mean ± SE mm	Range mm
Wing	61	118,95 ± 0,41	110-128
Tarsometatarsus	60	22,15 ± 0,19	0,2-26,8
Culmen	61	17,39 ± 0,10	6,0-18,8
Wing-span	56	367,48 ± 1,09	352-380
Tail	59	96,81 ± 0,53	87-107
Total length	55	231,96 ± 0,91	216-242

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* Birds older than eight months (see section under breeding behaviour)

Table 4 : Measurements of adult* red-billed oxpeckers collected and trapped in the Skukuza area during March 1973 - December 1974.

Dimensions	Number measured	Mean ± SE mm	Range mm
Wing	249	117,73 ± 0,20	107-128
Tarsometatarsus	248	22,42 ± 0,10	20,2-27,0
Culmen	249	17,07 ± 0,06	13,8-20,2
Wing-span	122	357,06 ± 0,77	340-380
Tail	224	95,60 ± 0,27	71-111
Total length	108	227,81 ± 0,66	212-259

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* Birds older than eight months (see section under breeding behaviour)

Table 5 : Measurements of immature* red-billed oxpeckers collected and trapped in the Skukuza area during March 1973 - December 1974.

Dimensions	Number measured	Mean ± SE mm	Range mm
Wing	92	115,25 ± 0,35	106-121
Tarsometatarsus	92	22,43 ± 0,20	17,5-27,3
Culmen	92	17,12 ± 0,07	15,8-18,8
Wing-span	19	356,63 ± 1,02	345-365
Tail	79	94,34 ± 0,38	87-101
Total length	20	226,80 ± 1,43	211-233

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* Free flying birds younger than eight months (see section under breeding behaviour)

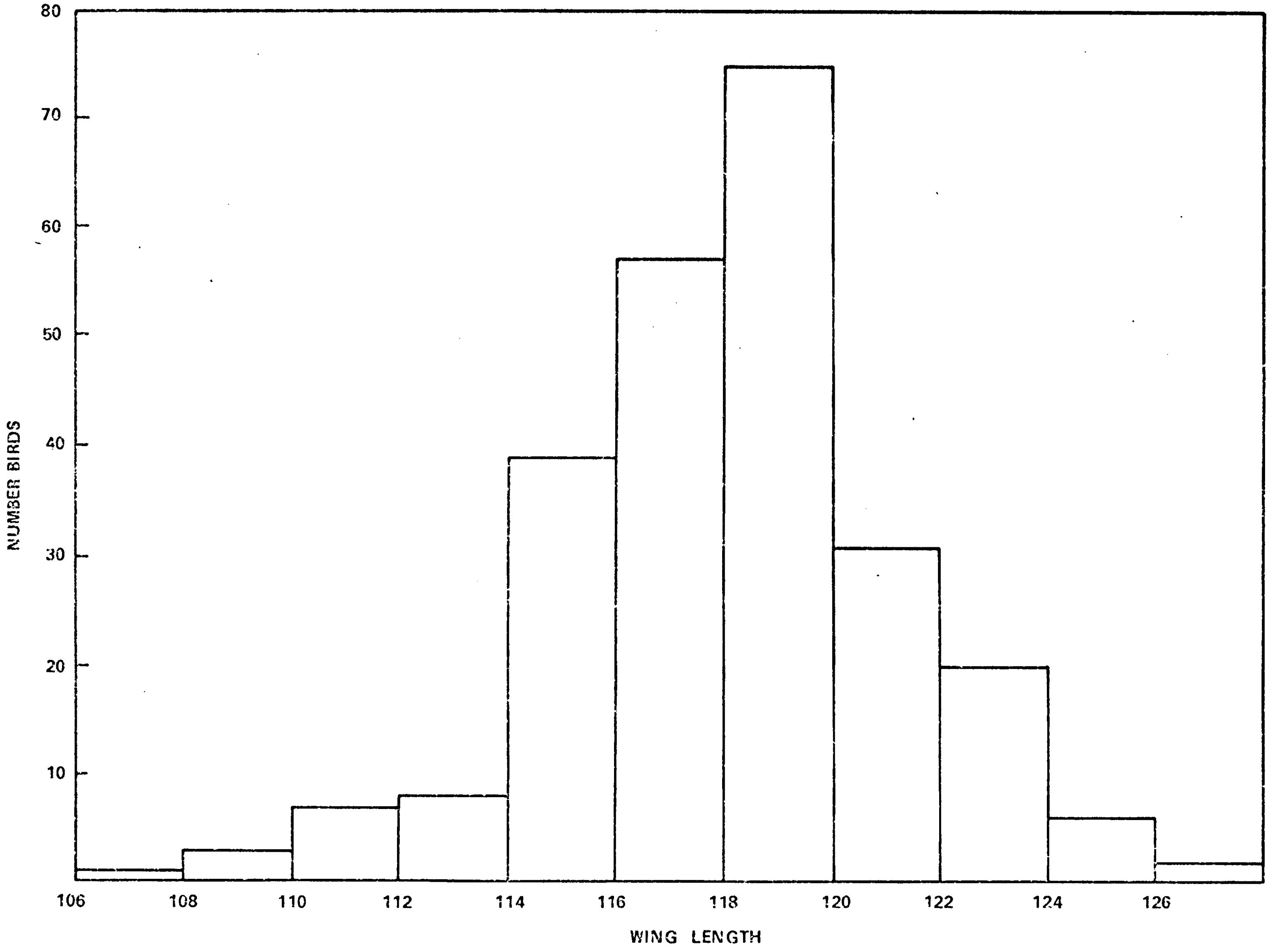

Fig. 2. Frequency histogram of wing measurements of adult red-billed oxpeckers trapped and collected in the Skukuza area during March 1973 - December 1974

the large range and overlap of measurements, size difference cannot be used as a practical method in sexing adult oxpeckers. The comparatively large range of measurements for the tail and wing may be the result of seasonal variation in length due to shortening by abrasion and parasite attack, especially when the birds are breeding, although birds with obviously worn or broken feathers were excluded from the analysis. This was found to be the case in the bronze mannikin (Lonchura cucullata) by Woodall (1975). The large range of measurements in total length could be the result from variation in the degree of straightening achieved in measuring the bird and is therefore not an accurate parameter.

The only statistically significant size difference between birds older than eight months (adult birds) and birds younger than eight months (immature birds) are wing- and tail-length (t-test, $P < 0,05$), the adult birds having a longer tail and wing. It can thus be speculated that tail and wing growth are not completed when the fledglings leave the nest. However, the coloration of the immature bird is a more accurate method to distinguish between adult and immature oxpeckers (see section under breeding behaviour). Furthermore, the age at which feather growth is completed, is not known.

Mass

Data on the mass of 342 red-billed oxpeckers weighed at Skukuza is summarised in Tables 6, 7 and 8.

There is very little recorded on the mass of birds in southern Africa and none was found to be published on the red-billed oxpecker (Liversidge 1968). The mean mass of an adult oxpecker was found to be 49,68g ($n = 250$, SEM = 0,24). A significant difference (t-test, $P < 0,05$) was found between the two age classes (birds older than eight months and birds younger than eight months), the adult birds being heavier with a mean mass of 49,68g compared to the mean mass of 45,89g for immature birds. No significant difference (t-test, $P > 0,05$) was found between the mean mass of the adult males and females.

Table 6 : Mass of adult and immature red-billed oxpeckers trapped and collected in the Skukuza area during March 1973 - December 1974.

Age	Number weighed	Mean ± SE (g)	Range (g)
Adult	250	49,68 ± 0,24	34-59
Immature	92	45,89 ± 0,41	35-86

Table 7 : Mass of adult male and female red-billed oxpeckers trapped and collected in the Skukuza area during March 1973 - December 1974.

Sex	Number weighed	Mean ± SE (g)	Range
Male	61	50,95 ± 0,33	45-56
Female	55	50,53 ± 0,43	42-59

Table 8 : Comparison of monthly mean mass of adult and juvenile red-billed oxpeckers trapped and collected in the Skukuza area in the period May 1973 - December 1974.

Month	Adult				Juvenile			
	Number weighed	Mean mass (g)	Standard deviations	Range	Number weighed	Mean mass (g)	Standard deviation	Range
1973 May	10	46,4	3,97	41-55	10	44,4	3,66	40-52
June	10	45,9	5,01	34-54	6	43,3	2,61	41-47
July	13	50,0	2,57	44-53	0			
Aug.	13	48,5	3,54	43-54	8	44,6	3,07	42-51
Sept.	10	49,6	2,70	45-54	3	41,3	2,07	40-43
Oct.	13	52,2	0,63	47-55	1	46,0	0	
Nov.	17	49,8	2,66	46-55	0			
Dec.	8	52,5	2,83	49-59	1	47,0	0	
1974 Jan.	16	49,7	2,28	45-55	3	45,6	2,51	45-46
Feb.	22	48,9	3,44	41-53	7	48,7	2,05	46-51
March	9	50,7	4,87	48-56	10	48,0	5,39	36-56
April	8	50,6	3,16	45-54	6	47,3	4,36	41-52
May	9	49,6	4,43	39-55	9	49,1	2,88	44-55
June	8	50,9	0,55	49-54	5	46,8	1,18	45-48
July	8	51,6	2,55	48-54	1	45,0	0	
Aug.	7	50,4	4,27	45-54	4	45,0	1,41	43-47
Sept.	13	47,9	4,35	42-57	10	45,9	3,27	41-52
Oct.	11	49,8	3,36	44-54	1	47,0	0	
Nov.	7	52,7	2,77	47-54	0			
Dec.	17	48,3	4,39	42-57	1	42,0	0	

Moreover, no significant difference (t-test, $P > 0{,}05$) was found between the seasonal variation in mass of the adult birds and adult sex groups in a comparison between the average mass in the winter and spring (May - October) and in the summer and autumn (November - April). Too few birds were weighed to justify an analysis and comparison of the variation in mass in the difference months of the year or time of day.

CHAPTER 5

GENERAL BEHAVIOUR

Introduction

Behaviour of a bird as defined by Pettingill (1970) is what it does and how it responds to its surroundings. There have been previous publications on various aspects of the behaviour of the red-billed oxpecker which are summarised by Attwell (1966). However, the general behaviour had not yet been studied in detail and it was therefore neccessary to first undertake this as a basis for the clarification of the biology of this species.

There are a number of behavioural aspects of oxpeckers not directly connected with social organisation or with breeding, although certain of the behaviour patterns may have acquired signal function and may therefore affect the social life of the birds to some extent. This aspect of behaviour is generally called individual behaviour and includes maintenance behaviour, concerned with the care and comfort of the body, and behaviour associated with selection of habitat, cover and food and with feeding. This chapter refers thus only to the individual behaviour of the oxpecker while some aspects of the social behaviour are given in the section under breeding biology. Although the feeding methods of the oxpecker are described in this chapter, the feeding ecology is discussed elsewhere (Stutterheim in prep.).

Most of the data on drinking behaviour of oxpeckers were collected at the Renosterkoppies and Shiloweni dams and the total observation time at these dams amounted to 56 h, which consisted of four full days of observation (Fig. 1).

Results

Maintenance activities

Locomotion

On the ground

Locomotion on the ground is either by hopping or by walking and running. The bird normally hops with both feet together, with the tip of the tail making contact with the ground. Except when drinking water, oxpeckers were only observed on the ground in the close vicinity of their mammalian symbionts.

On the mammals

Locomotion on the symbionts is either by hopping, walking or climbing. Walking and hopping are only used on the horizontal surfaces of the symbionts. When climbing on the mammals, the sharp curved claws of the feet are used for clinging onto the skin of the mammal. However, by changing only one foot at a time, the oxpecker can utilise any surface area on the symbiont. In the climbing process the tarsometatarsus of the bird is in contact with the symbiont and the long tail is used as a brace. Birds in captivity were unable to stay put on any vertical surface if they were unable to reach and to cling on to a skin surface embracing a thick pelage.

Aerial

The flight of the oxpecker is characteristically direct but undulating, which appears to be a flap followed by a glide. The climbing flight consists of deep wing strokes until the preferred height is reached. The steady horizontal flight is at least 200 m above ground level. The descent for landing is either gradual or circling. The tail is spread just before landing on a symbiont and is thus used as an airbrake. Oxpeckers were also observed to hover for short periods of time when pursuing slow flying insects. When hovering the tail is typically spread and depressed. According to Pennycuick (1972) this has two effects - in the first place some supplementary wing area is provided, and secondly the action of the tail helps to suck air downwards over the central portion of the wing, thus increasing the maximum lift coefficient of the wing itself. Both effects enable the bird to remain airborne, and under control, at lower speeds than would otherwise be possible.

From a total of 36 observations, 76% of the oxpeckers landed on mammalian symbionts on which birds were already present - probably to avoid intolerant individuals (Stutterheim in prep.).

Feeding methods

The actual feeding methods of each bird depend on the type of food being eaten. The following feeding methods have been distinguished.

Scissoring

In scissoring the tip and sides of the bill are used when tick or wound feeding, by pushing a rapidly opening and closing bill through the hair or over any other body area of the mammalian symbiont. In lateral scissoring the head is parallel to the body of the symbiont. However, the angle of scissoring, from vertical to lateral, depends on the surface being utilised. Vertical scissoring can also be described as nibbling because it is seldom done with a sweeping movement (Plate 5). As suggested by Van Someren (1951), scissoring is a feeding method based on touch and not by sight, since indiscriminate surveys are made in any area of the hide before the birds move on to a new area and any small objects stuck in the hair are swallowed. After every scissoring movement the head is lifted and the collected material is swallowed, as indicated by a slight opening and closing of the bill.

When scissoring, the eyes are not closed while the tip of the tail is in contact with the body of the mammalian symbiont. In lateral scissoring the one leg is always directly underneath the body with the tarsus making contact with the body of the symbiont. The other leg is usually at an angle of 45° away from the body. In vertical scissoring or nibbling, both legs are directly underneath the body of the bird.

Plucking

This is a feeding method where eye-sight plays an important role. The body of the mammalian symbiont is searched

Plate 5. Lateral scissoring by the red-billed oxpecker on an impala, September 1974.

36-i

with a head that is turned sideways. Any visible ticks or loose pieces of skin are seized with the tip of the bill and collected with a backwards and turning movement of the head (Plate 6). During plucking both legs are placed directly underneath the body while the tip of the tail is in contact with the body of the symbiont. The eyes are not closed during plucking.

Pecking

Pecking is mainly used for sore feeding. Pecking can be described as a pickaxe-like action with a slightly opened or closed bill (Attwell 1966). During pecking both legs are placed directly beneath the bird's body while the tip of the tail is in contact with the body of the mammalian symbiont. After a few pecking movements the bird is usually forced to stop and swallow any collected material. Pecking is usually followed by vertical scissoring in wound feeding for collecting any free flowing serum or blood.

Insect catching

Three different methods are used:

hawking

The bird flies or jumps into the air and catches an insect away from the mammalian symbiont with a snapping movement of the bill. Slow moving insects are followed with a hovering flight. The bird always returns to the same mammal. The birds are not very adept at this aerial hunting and appear to miss frequently.

random catching

The birds snap at any insect within reach on the mammalian symbiont. In random catching a bird would suddenly stop an activity, snap at an insect and proceed with the activity.

stalking

The bird lowers its body, points its bill at the insect and in this position, suddenly runs forward and by shooting out its head, catches the insect on the body of the mammalian symbiont.

Plate 6. An adult red-billed oxpecker collecting ticks by means of plucking from the hind leg of a buffalo at Skukuza, September 1974.

38-i

Insects are swallowed at once if very small, but usually they are nipped to kill them. Larger insects are softened by being run back and forth through the bill and squeezed at each step. Birds in captivity were observed to soften hard insects by hitting them against a hard surface.

Drinking behaviour

Drinking posture

The red-billed oxpecker utilises any available surface water. When drinking the birds sit next to the water with the tail and tarsus in contact with the ground. The head is lowered and a slightly opened bill is dipped into the water with a subsequent lifting of the head. The eyes are not closed while drinking and the tail is not lifted from the ground when the head is lowered. From a total of 39 observations the mean time spent on the ground was 40 sec (SD = 89,4, range = 15-83) and the mean number of times the bill was dipped into the water, six (SD = 9,8, range = 2-9).

Oxpeckers were frequently observed drinking from human-made structures like reservoirs and drinking troughs. Oxpeckers were also observed drinking directly from a stream of water from a pipe at a drinking trough, when the water level was too low and could not be reached. This behaviour seems to be adopted by learning, because a juvenile bird was observed sitting next to this jet of water without drinking and only started drinking when an adult bird was drinking from the pipe. However, the birds prefer drinking from the trough. When a drinking trough is nearly empty and the water cannot be reached in the usual way, the head is turned sideways and the water is picked up by a scissoring movement of the bill.

After drinking, oxpeckers fly to any mammalian symbiont present. The water drinking behaviour is usually followed by a short period of resting or by comfort movements.

Utilisation of water

The utilisation of Renosterkoppies dam by the red-billed oxpeckerand their mammalian symbionts is summarised in Table 9/ Figs. 3,4 and 5.

These data were analysed statistically and a test on the coefficient of correlation between the different variables showed that there is a significant relationship (t-test, $P < 0{,}05$) between the number of birds and the number of mammalian symbionts that utilised Renosterkoppies dam in June 1974. A significant correlation (t-test, $P < 0{,}05$) was also found between the number of oxpeckers and the biomass of the mammalian symbionts that exploited the dam in June. Moreover, a more significant correlation was found between the number of oxpeckers and the biomass of the mammalian symbionts that exploited the dam ($rs = 0{,}78$) than between the number of oxpeckers and the number of symbionts ($rs = 0{,}65$). It can thus be concluded that the mammalian species and the size of the mammalian species utilised by the oxpeckers, play an important part in their drinking behaviour.

This is clearly seen in the methods used by oxpeckers to approach a water point e.g.:

a. By riding on a mammal to the water.

b. By flying to the water and utilising any mammals present.

c. By flying to the water and, if no symbionts are available, it sits in a tree and waits for symbionts to approach the water. Oxpeckers were observed sitting in a tree for nearly 30 min before flying down to the water in the absence of any mammalian symbionts.

The mammalian symbionts present at a water point are used as a platform from which the bird flies down to the water and back after drinking. This behaviour can probably be linked with anti-predator behaviour. If any predator is observed by the birds, the alarm call is given and all the birds immediately fly back to the symbiont. Birds appear to stay for longer periods on the ground in the vicinity of

Table 9 : Utilisation of Renosterkoppies dam by the red-billed oxpecker and their mammalian symbionts in June 1974.

Time	Number birds	Number mammals	Biomass of mammals in kg*	Ambient temperature in °C
06h00 - 06h30	0	0	0	12,0
06h30 - 07h00	1	0	0	12,3
07h00 - 07h30	38	2	1320	11,8
07h30 - 08h00	70	18	2604	13,8
08h00 - 08h30	66	20	800	16,0
08h30 - 09h00	58	94	5062	18,0
09h00 - 09h30	37	31	2188	20,5
09h30 - 10h00	44	34	1360	22,0
10h00 - 10h30	36	100	4816	23,9
10h30 - 11h00	72	47	8262	25,0
11h00 - 11h30	106	32	7554	25,5
11h30 - 12h00	52	5	820	27,0
12h00 - 12h30	100	21	2090	28,3
12h30 - 13h00	35	9	360	29,0
13h00 - 13h30	56	5	200	30,0
13h30 - 14h00	94	4	2020	28,0
14h00 - 14h30	30	5	210	28,6
14h30 - 15h00	63	1	660	29,0
15h00 - 15h30	59	4	160	29,0
15h30 - 16h00	7	0	0	28,0
16h00 - 16h30	8	1	40	27,2
16h30 - 17h00	0	0	0	24,0
17h00 - 17h30	1	0	0	22,0
17h30 - 18h00	0	0	0	19,0
n	1016	432	39998	
Range	0-106	0-100	0-8262	12-30

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* As given by Pienaar (1966)

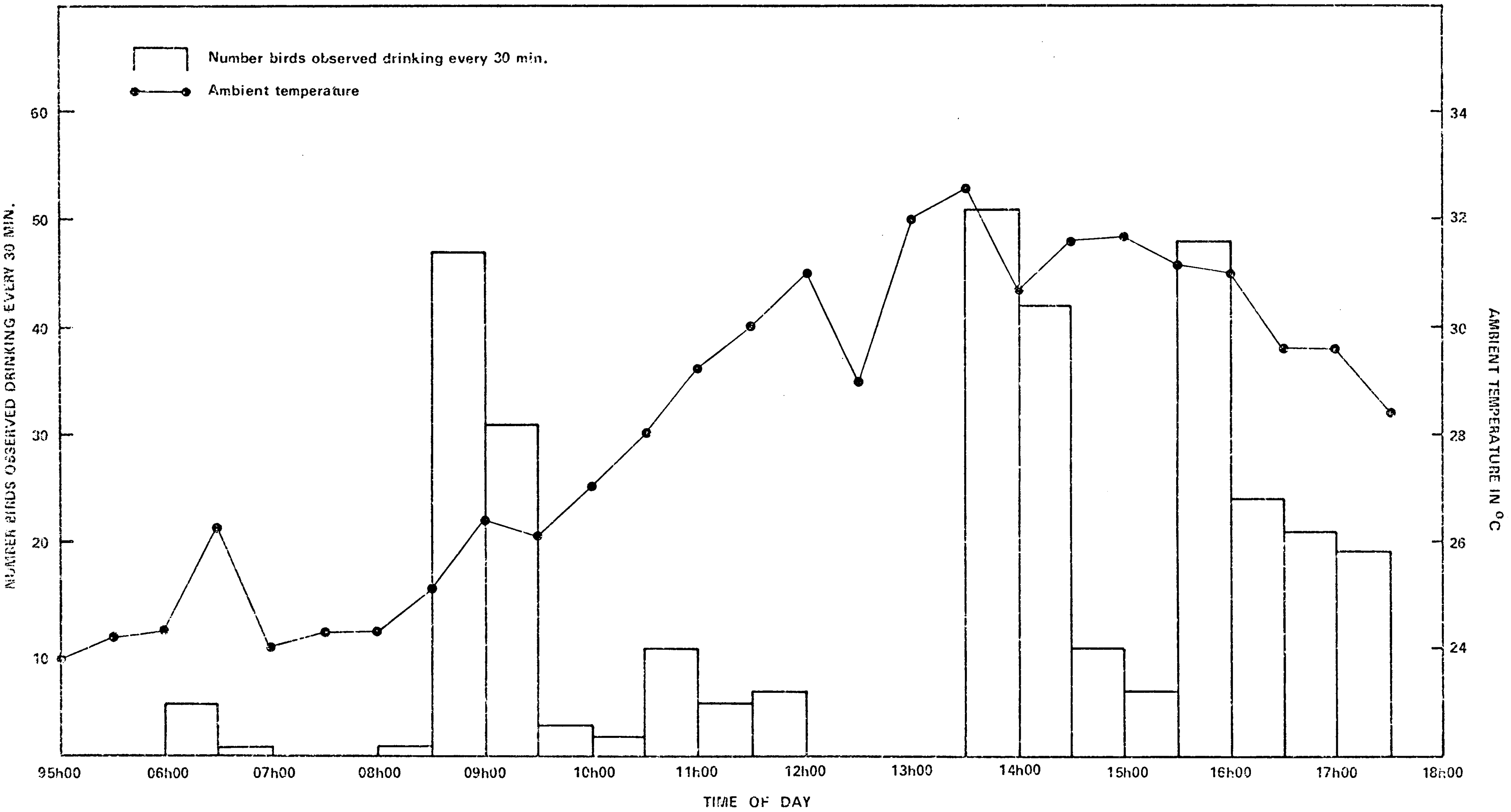


Fig. 3. Relation between the drinking behaviour of the red-billed oxpecker and ambient temperature at Renosterkoppies dam in March 1973

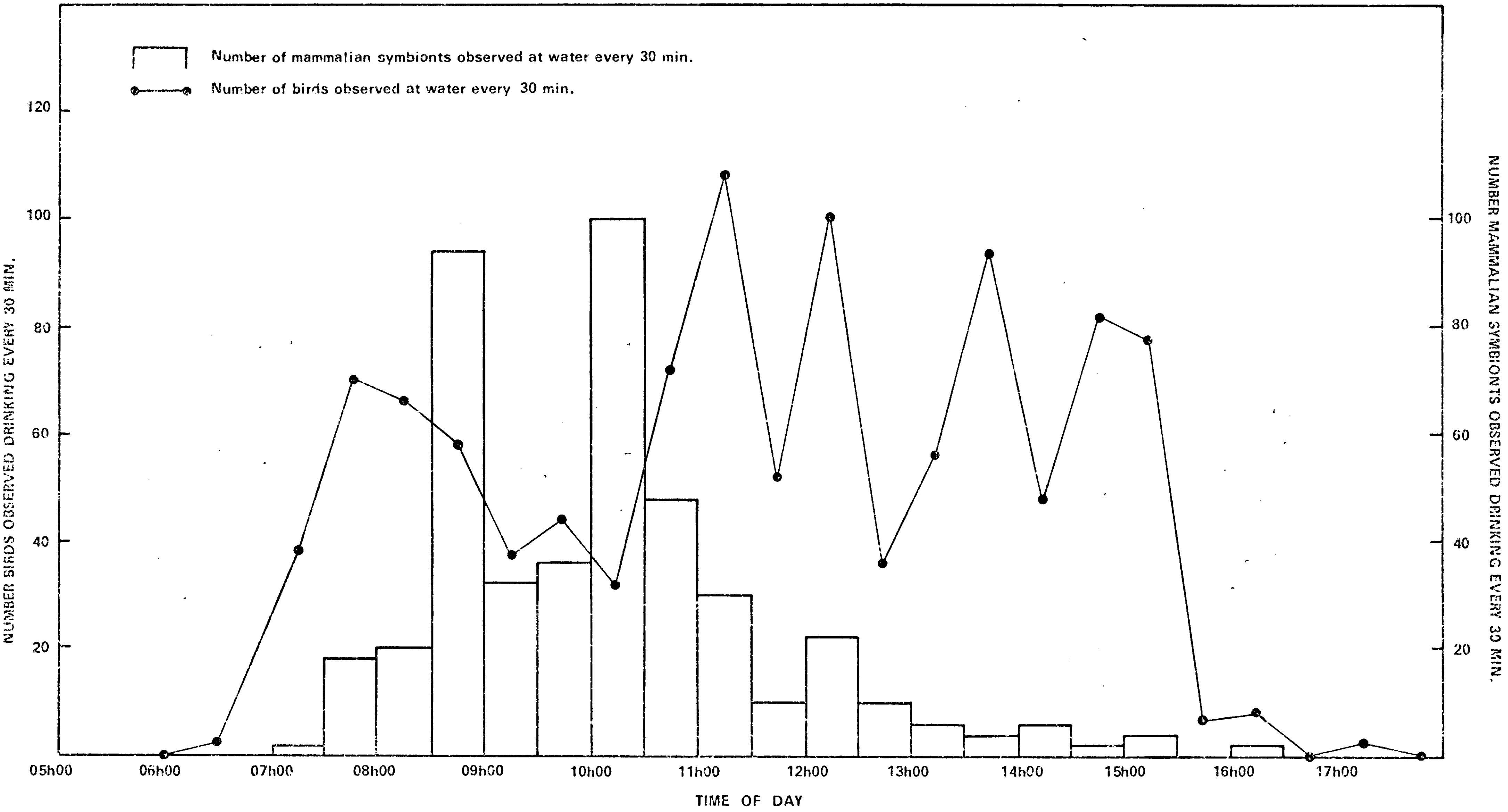


Fig. 4. Relationship between the number of oxpeckers and number of mammalian symbionts that utilised Renosterkoppies dam on 26 June 1974

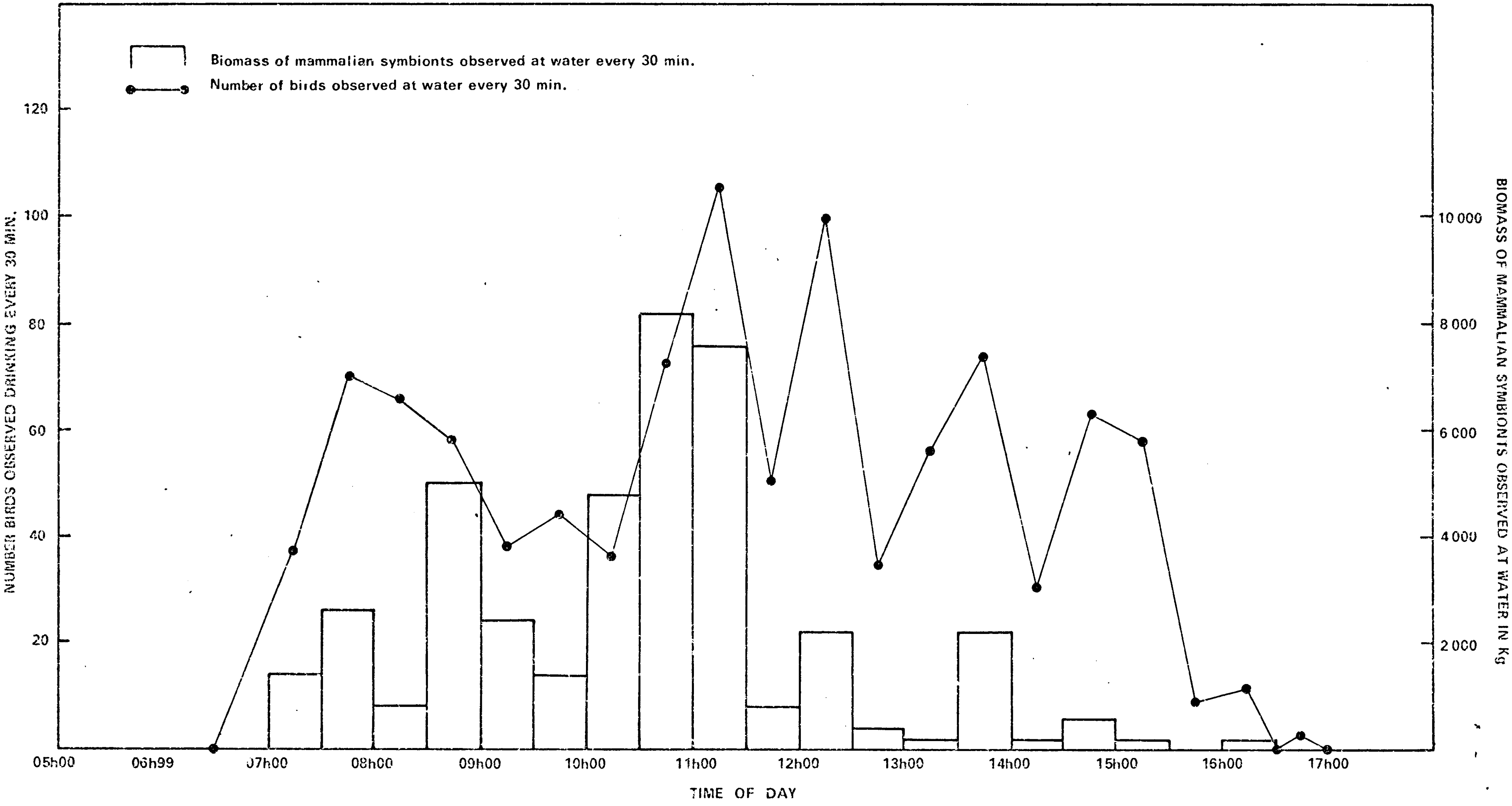


Fig. 5. Relationship between the drinking behaviour of the red-billed oxpecker and the biomass of the mammalian symbionts observed at Renosterkoppies dam on 26 June 1974.

mammals than birds that are drinking in the absence of a symbiont. Birds drinking in the absence of a symbiont usually look around before drinking. This behaviour was not observed in the vicinity of a symbiont.

No significant correlation (t-test, P> 0,05) was found between the number of oxpeckers that utilised Renosterkoppies dam in June 1973 and ambient temperature. With a significant correlation between the number of mammalian symbionts and number of oxpeckers that exploited Renosterkoppies dam, however, it can be speculated that oxpeckers utilise available water about the same time as their symbionts (Fig. 4).

The first birds arrived about an hour after sunrise and the last birds about two hours before sunset. Young (1970) summarised the utilisation of water by the larger mammal species in the Kruger National Park. Zebra and wildebeest drink mainly during the daytime and normally between 09h00 and 12h00. Although buffalo can drink at night, the main drinking period is between 06h00 and 21h00. Impala drink mainly during the day with a peak between 09h00 and 12h00 in the winter months and 09h00 and 21h00 during the summer months. Counts made at Renosterkoppies dam indicate that giraffe appear to drink between 07h00 and 15h00 in the winter months. As indicated by Young (1970) and from the counts made at Renosterkoppies dam, a high percentage of the larger mammal species appear to drink between 09h00 and 12h00, although some game do drink after 12h00. A count made at Renosterkoppies dam during June 1974 indicated that 88% of the mammals and only 57% of the birds drank between 09h00 and 12h00 (Fig. 4/Table 9). During March 1974 only 33% of the birds utilised Renosterkoppies dam between 09h00 and 12h00. However, only 24% of the birds during June and 9,6% of the birds during March drank water in the absence of any mammalian symbionts. It can thus be concluded that although there is a decrease in the number of mammalian symbionts that visit water points after 12h00, there are still enough symbionts present to be utilised by the oxpeckers. With less mammalian symbionts present the association is increased. In impala the relationship was 1,1 birds per animal during

09h00 - 12h00 and 2,2 birds per animal after 12h00 during June 1974 at Renosterkoppies dam which indicate a statistically significant ($P < 0{,}05$) increase in the mammal relationship.

Captive birds fed on a mixture of mince meat, "Pro Nutro" and egg yolk, drank water between four and six times a day. Table 9 indicates that during June 1974 a total of 1016 oxpeckers were observed drinking at Renosterkoppies dam. However, the total number of oxpeckers in the Skukuza/ Tshokwana area was calculated as 6336 (Stutterheim in prep.). It is apparent that it is impossible that 16% of the total population to have been concentrated around Renosterkoppies dam and it can thus be speculated, as marked birds were not used, that oxpeckers in the wild drink water more than once every day. Since almost any bird may drink under some circumstances, to assess the importance of availability of free water for the maintenance of water balance, it is really necessary to perform the simple experiment of keeping live specimens without water and monitoring their changes in body weight and their survival times (Cade 1965). An experiment of this kind will probably indicate the minimum amount of water needed by the oxpecker to maintain its water metabolism.

Although the food preferences of the oxpecker indicate a high water content it appears that the birds do not have effective physiological mechanisms for water conservation. This is compensated for by visiting water sources and by remaining inactive in the shade during the hot part of the day (see section under thermoregulatory behaviour). Oxpeckers are potentially much more mobile vertebrates than their mammalian symbionts. It can thus be speculated that they rely more on behavioural modifications than physiological adaptations in maintaining their water balance.

The water requirements of the red-billed oxpecker could be a factor determining the distribution and abundance of the species. A total of 332 birds were counted in a 12h period during March 1974 and a total of 1016 birds in a 12h period during June 1974 at Renosterkoppies dam. This indicated a concentration of oxpeckers at the more permanent water points during the winter months. However, Renosterkoppies dam completely dried up in early July 1974. This resulted in a complete disappearance of the larger mammal species and oxpeckers from the Renosterkoppies dam area. However, as they utilise water dependent mammalian species (Stutterheim in prep.; Young 1970), water will be available if their mammalian symbionts are available.

Table 10 shows the relationship of oxpeckers and mammals in a radius of 500 m from open surface water compared to the relationship farther than 500 m from water in the Skukuza/Tshokwana area from March to September 1973. These results were obtained in counts consisting of 17783 mammals and 2088 oxpeckers. A two-way analysis of variance showed significant differences ($F0{,}05 = 3{,}87 < 7{,}21$ and $F0{,}05 = 5{,}59 > 3{,}20$) in the relationship of the oxpeckers with the nine different mammal species near or away from open surface water. Further, in an analysis for the confidence interval for proportions, a significient difference ($P < 0{,}05$) was found between the mean mammal relationship of the oxpeckers near or away from water. Table 10 indicates that the association increased from 0,078 birds per mammal away from water to 0,2 birds per mammal in a 500 m radius around water in the Skukuza/Tshokwana areas from March to September 1973. It can thus be concluded that with a concentration of oxpeckers around water, an increase in the association with mammals occurs.

In the absence of a "preferred" host around water, oxpeckers utilised normally unused symbionts. Table 10 indicates that the association with warthog increases from 0,041 - 0,2 birds per mammal around a water point and the association with wildebeest increases from 0,069 - 0,17 birds per mammal. However, non-symbionts like elephant and tsessebe are not utilised by the red-billed oxpecker even in the absence of other symbiont species (Stutterheim in prep.).

Table 10 : Relationship of the red-billed oxpecker and mammals in a radius of 500 m from open surface water compared to relationship farther than 500 m from water in the Skukuza/Tshokwana area from March to September 1973.

	Relationship near water			Relationship away from water		
	Number mammals	Number birds	Birds per mammal	Number mammals	Number birds	Birds per mammal
Impala	1917	163	0,08	15412	527	0,034
Blue wildebeest	176	30	0,17	376	26	0,069
Zebra	573	133	0,23	1012	128	0,126
White rhinoceros	2	4	2,0	12	13	1,083
Giraffe	37	284	7,6	352	579	1,645
Kudu	11	11	1,0	290	54	0,186
Sable antelope	42	52	1,2	61	53	0,869
Warthog	50	10	0,2	268	11	0,041
n	2808	687		17783	1401	
$\bar{x}$			0,2			0,078
Range			0,08-7,6			0,034-1,645

Comfort movements

Where possible terminology follows that employed by McKinney (1965) for the Anatidae.

Stretching movements

wing-and-leg-stretch

The bird's mass is shifted onto one foot while the other foot is extended behind and a little to one side with the wing on the same side extended backwards over the foot (Plate 7). The head is pushed slightly forward and downward and turned to the side of the stretch. The rectrices on the stretch side is also fanned.

double-wing-stretch

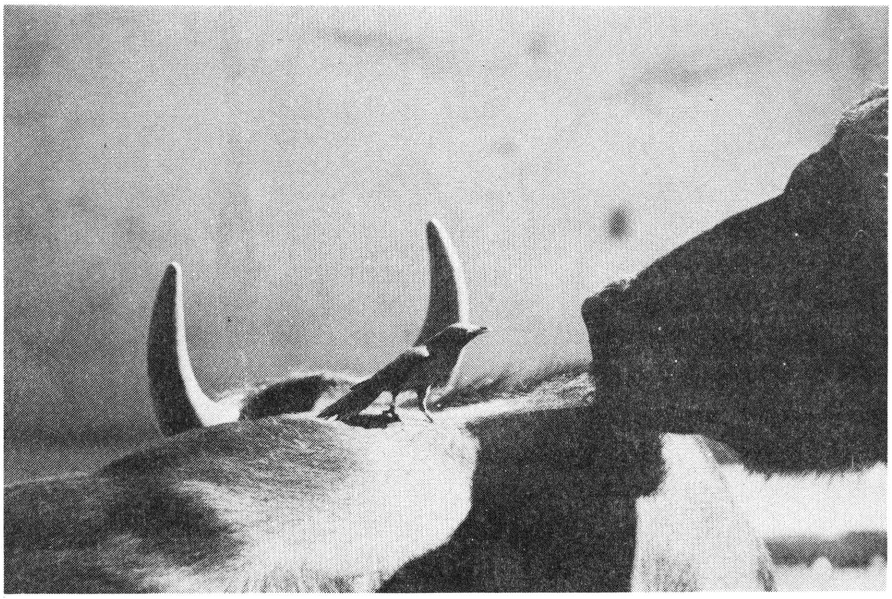
The wings, while remaining bent at the carpal joint, are raised upward until the scapulars of both sides touch above the back. Simultaneously, the neck is stretched forward and down. Double-wing-stretch commonly follows wing-and-leg-stretch and occurs usually after a period of resting or sleeping and before preening.

jaw-stretch

The bill is opened wide for a few seconds and closed again. It is usually performed when the bird is resting. Other movements involved opening of the bill are probably not related to jaw-stretching. Birds which have material stuck in the mouth or throat will frequently open the bill, shake the head and scratch. Regurgitation was not observed in the red-billed oxpecker as suggested by Van Someren (1951) to get rid of the hair collected in the stomach. Regurgitation of pellets was also not observed in birds in captivity that were feeding on a donkey.

Cleaning movements

Plate 7. The wing-and-leg-stretch of the red-billed oxpecker on the back of a buffalo at Skukuza, June 1974.



scratching

In head-scratching the bird stands on one leg, the head is bent back to one side, the wing on that side is dropped slightly, and the foot on that side is brought up behind the wing to scratch the head. During head-scratching the bill is slightly opened and the eyes are closed. Head-scratching in the oxpecker is indirect in that the foot is brought up over the wing as in most passerines (Simmons 1957). In scratching the tip of the tail is in contact with the mammalian symbiont. The claw on the middle toe appear to be the scratching tool.

bill-cleaning

Bill-cleaning consists of wiping the bill quickly on an available hard surface. The mean number of wiping strokes was calculated as four (n = 19). Bill-cleaning is usually observed during or just after feeding and always after drinking. Surfaces utilised for bill-cleaning were the horns of mammalian symbionts, branches of trees, hooves of symbionts, the hard skin of rhino and the upper hard surface of the bull giraffe horn. Birds on symbionts without any horns were observed to fly to a nearby tree for bill-wiping.

chin-rubbing

Chin-rubbing usually occurred in combination with bill-cleaning. In chin-rubbing the bird bends forward, turns the head sideways and rubs the chin on any available surface. During chin-rubbing the eyes are closed.

foot-pecking

During foot-pecking the foot is brought forward and held up while it is nibbled with the bill. This movement was only observed twice and appears to be a direct response to an irritation on the foot.

bathing

Bathing is done in shallow water after drinking and only in the presence of a mammalian symbiont. In the red-billed oxpecker there are three main bathing movements:

head-dipping, wing-thrashing and tail-shaking. During bathing the breast and back feathers are fluffed. When a bird begins to bathe, head-dipping is the first action. The head is dipped so that the neck and chin feathers just touch the water. The bird then half rises out of the water and rapidly beats the partly opened wings on the surface of the water while the tail, which is fanned out, is shaken from side to side. This sequence is repeated several times during bathing. When no shallow water was available, oxpeckers were observed to turn away from the water, dip the tail into the water and perform the wing-thrashing and tail-wagging movements. After bathing the birds always flew back to their mammalian symbionts for preening and drying.

dust-bathing

In dust-bathing the bird lies on its breast and with thrashing movements of the wings, shuffels in the dust with side to side movements of the body. During intervals between wing-thrashing the bird would rub the chin in the dust with a forwards and backwards movement. During dust-bathing the abdomen, breast, rump, head and neck feathers are fluffed. Loose ground or sand is preferred for dust-bathing. However, an oxpecker was also observed performing dust-bathing movements on the rump of a rhino. This specific rhino had had a mud-bath previously and was covered with dry mud which could have provided the stimulus for dust-bathing. The red-billed oxpecker was only observed dust-bathing in the presence of their mammalian symbionts.

Preening

According to McKinney (1965) the term preening is used for activities which involve contact of the bird's bill or head with the feathers in the form of billing, rubbing or combing movements. Three types of preening can be distinguished in the oxpecker: oiling, nibbling and wet-preening after bathing. As it was difficult, at times, to distinguish between oiling and nibbling these are discussed under the same heading. Bathing is normally followed by oiling during wet-preening but oiling also occurs without being preceded by bathing.

oiling and nibble-preening

During nibble-preening the bird may pause in the region of the preen gland. The gland is then nibbled with the tip of the bill before proceeding with nibble-preening or oiling. All regions of the body are preened but for the head and upper neck. The oiling or nibble-preening procedure can be described as follows:

remiges

The remiges are preened in a typical fashion, with the wing held out partly open and at right angles to the body, a feather is nibbled at the base and then by a lifting movement of the wing pulled through the beak.

rectrices

When preening the tail, the rectrices are held to one side and slightly fanned, the feather is then nibbled on the ventral side before being pulled through the beak. In preening the rectrices feathers,the rump is fluffed.

other body regions

Usually it appears to be the skin or bases of the feathers which are nibbled before combing a feather. The area being preened is also usually fluffed. Neck, breast, abdomen, back and rump feathers were preened by lowering the head or turning the head around. The underwing coverts are preened with the wing held out partly open and at right angles to the body. Wingface-preening, involving the outer surface of the wing, is done by lifting the wing and turning it sideways and by turning the head around.

wet-preening

Bathing is always followed by a session of wet-preening on a mammalian symbiont. The procedure of wet-preening is the same as in oiling or nibbling, except that every preening session is followed by wing-shaking and tail-shaking. Shaking could be to remove most of the water from the plumage. In wet-preening the tail is fanned and the back and rump feathers fluffed.

Shaking movements

body-shake

The plumage is erected before the whole body is shaken. The wings remain in the pockets formed by the breast and flank feathers. The head is lowered during body-shake. The body-shake is given typically after oiling and nibbling.

wing-shake

The wings are slightly drooped and shaken vigorously. The head may be lowered during wing-shaking. During wing-shaking the wings are partly opened. The wing-shake occurs after resting and during bathing and wet-preening. In the wing-shake during wet-preening the body feathers are fluffed and the tail is fanned.

tail-shaking

The tail is fanned and shaken from side to side several times. Tail-shaking may be very brief, lasting only one or two seconds. Tail-shaking occurs in bathing and wet-preening. The primary function is apparently the removal of water from the tail but at times the movement is given as a direct response to water on the tail.

Thermoregulatory behaviour

Heat loss behaviour

An important factor that could influence the activity of the red-billed oxpecker and its mammal relationship is ambient temperature. In the period March 1973 - December 1974, from a total of 1034 observations, a highly significant correlation (t-test, $P < 0,05$) with $r_s = 0,92$, was found between the ambient temperature and the percentage birds in the shade. Moreover, a highly significant negative correlation (t-test, $P < 0,05$) was found between the ambient temperature and the percentage birds in the sun. This correlation is shown in Fig. 6/Table 11 which indicates that with an increase in the ambient temperature, oxpeckers favour shade and with a decrease in ambient temperature or at low ambient temperatures, oxpeckers move into the sun. It can thus be concluded that at high ambient temperatures, oxpeckers prefer mammalian symbionts in the shade and at low ambient temperatures, symbionts in the sun. Oxpeckers active in the sun at high ambient temperatures (above 35° C) were observed to pant with an open bill. No gular fluttering was observed. Panting was accompanied by depressing the plumage and holding the wings away from the body.

Heat conservation behaviour

The body plumage is fluffed out, the wings held close to the body, the legs covered by the abdominal feathers while the birds sit flat on the mammalian symbiont. The head is also pulled well down between the shoulders.

Sunbathing

Sunbathing was observed in both the standing and sitting position on the back or head of a mammalian symbiont. The bird would orientate itself with the back directed to the sun's rays, droop both wings and turn the head sideways towards the sun. In sunbathing the bill is opened, the eyes are closed and the crown and rump feathers are fluffed. Oxpeckers were also observed sunning themselves on the symbionts with a fluffed out plumage in the early morning shortly after sunrise. As pointed out by Kemp (1972), birds sunbath only when completely at ease, and this is rarely seen in the field.

Resting, sleeping and roosting behaviour

Between feeding, oxpeckers were often observed resting on their mammalian symbionts. When at rest the body is

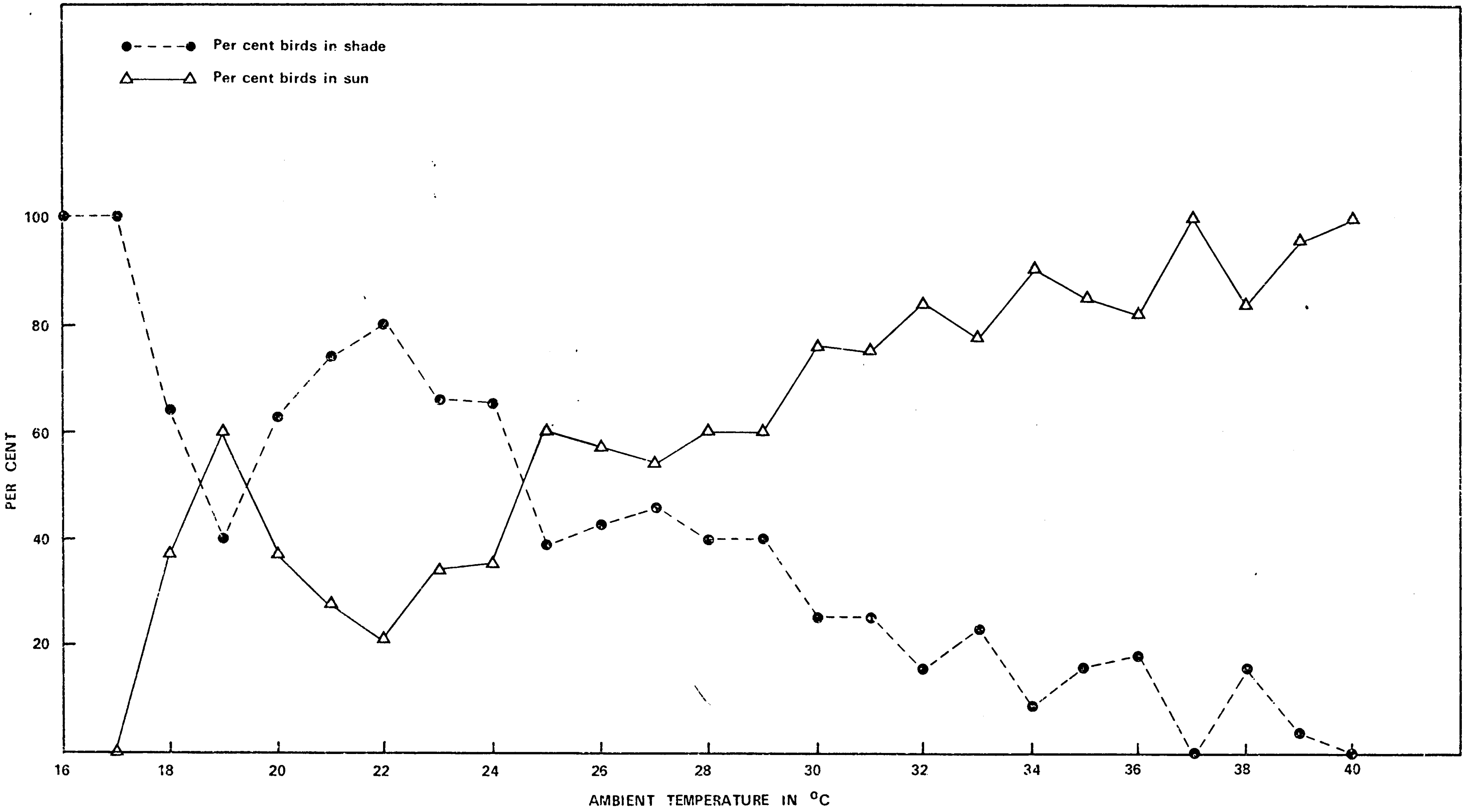


Fig. 6. Per cent of oxpeckers in sun and shade as related to ambient temperature in the Kruger National Park as recorded from March 1973 until December 1974.

Table 11 : Occurrence of the red-billed oxpecker on their mammalian symbionts in the sun or shade as related to ambient temperature in the Kruger National Park, observed in the period March 1973 - December 1974.

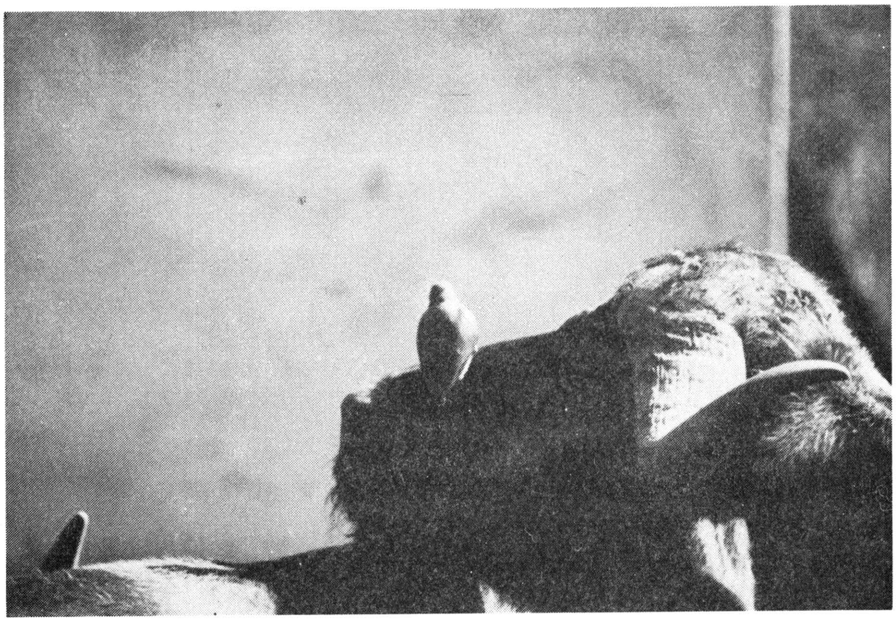
Ambient temperature in °C	% Birds in shade	% Birds in sun	Number sightings
16	0	100	5
17	0	100	8
18	37	63	8
19	60	40	5
20	37	63	16
21	28	72	42
22	21	79	19
23	34	66	29
24	35	65	31
25	61	39	31
26	57	43	35
27	54	46	66
28	60	40	38
29	60	40	69
30	76	24	71
31	75	25	97
32	84	16	100
33	77	23	116
34	91	9	67
35	84	16	83
36	82	18	34
37	100	0	11
38	84	16	19
39	96	4	29
40	100	0	5
n			1034

lowered so that the abdominal feathers cover the feet, the head is pulled well down between the shoulders, with the bill pointing forward (Plate 8). Oxpeckers prefer inactive symbionts in the shade for resting purposes (see section under thermoregulatory behaviour).

Previous authors have mentioned that oxpeckers roost colonially in trees, reed beds, palms, on rocks, on roofs of buildings and on their mammalian symbionts (Van Someren 1951, Dowsett 1968, MacLachlan and Liversidge 1970, Mundy and Cook in press). Only two roosting localities were found in the Kruger National Park - one at Letaba camp and the other at Shingwidzi camp. Both these roosts were in a cluster of ilala palms (Hyphaene orinita). These roosts were 12 and 15 m above groundlevel respectively.

At the Shingwidzi roost the first birds arrived at the roost at 17h25 (about half an hour before sunset) during October and settled in a tree 50 m from the roost. This group was joined by another group and after giving the contact call (Stutterheim in prep.), both these groups flew into the roost. For every group of birds arriving, the contact call was given which was immediately answered. After circling the roost a few times these birds also settled in the roost. The last group arrived at the roost at 18h14. The birds roosted on top of the palm leaves and appeared to disperse in the cluster of palms. After settling in the roost, no birds were visible. The roosting birds were completely silent after dark, and left the roost at 05h05 (about 20 min after first light). The oxpeckers suddenly started giving the contact call, flew up in the air and after circling the roost a few times, dispersed in their different groups. A total of 19 birds utilised this roost and the mean size of the groups arriving at the roost was 2,1 (n = 7, SD = 6,9). No other bird species were observed utilising the palms at Shingwidzi, for roosting purposes.

Plate 8. The resting posture of the red-billed oxpecker on a buffalo at Skukuza, June 1974.



The roost at Shingwidzi is known to have existed for at least two years (Pretorius pers. comm.*). It can thus be speculated that the red-billed oxpecker have permanent roosting areas. The same was found by Mundy and Cook (in press) at a roost in northern Nigeria. According to Van Someren (1951) oxpeckers (species not stated) pile in on top of one another at roosting time. No evidence for this behaviour was found, although it was impossible to observe the birds after they had settled on the palm leaves. The sleeping posture was only observed in birds in captivity. Two postures were observed:

a) The bird would lower its body, fluff the crown, back and rump feathers, turn the head around and tuck its bill into the back feathers.

b) The bird would lower its body, the head is pulled well down between the shoulders and the bill is pointed forward. In sleeping, the eyes are closed but the birds were observed to rouse briefly from time to time.

No account can be given of a seasonal variation in the number of roosting birds. Mundy and Cook (in press) found that the size of the roost declined rapidly with the onset of the wet season which is probably a breeding dispersal. As no actual pre-roost gatherings (except for the first few birds) were observed at the Shingwidzi roost, the contact call given by the roosting birds appears to advertise the roost. According to Zahavi (1971) the type of advertisement of the gathering is adapted to minimise predation and pre-roost gatherings may increase predation pressure. The oxpecker seems to provide a further example of this phenomenon as no pre-roosting gatherings were observed. The birds only gave the contact call when a group arrived at the roost.

Roosting birds generally have two main requirements: protection from predators and shelter from adverse weather (Cullen 1964). Zahavi (1971) demonstrated the importance

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of roosting in a large compact group as a defence against predators. He found that it was much more difficult to catch a bird from a flock than a solitary bird because an alarm call would start a chain reaction which would disturb the whole flock. However, this was found not to be the case in the cattle egret (Ardeola ibis) (Siegfried 1971b). He found that the response of roosting cattle egrets to a potential predator, unless intruding disturbance is very obvious, does not normally involve synchronised mass communal action. On the other hand, Zahavi (1971) has put the anti-predator role into a different perspective. In discussing the evolution of communal roosting he suggests that the anti-predator adaptations found in roosts are secondary, being consequent upon the increase in predation-pressure when birds begin to assemble for the benefit of social food-finding. Zahavi (1971) and Mundy and Cook (in press) suggested that communal roosting serves the function of directing birds' attention to a good food supply on the following day; in the morning, birds which lack good feeding places, follow birds which know of good feeding sites. This is in line with Wards' (1965) hypothesis that birds which are seeking information on patchy and localised food can more efficiently do so from a communal roost.

Observations on the oxpeckers disagree with this hypothesis. Oxpeckers feed on very mobile mammals which may be widely scattered throughout the area. During the roosting period, these mammals can move a considerable distance (Young 1970). It can thus be speculated that a bird which had a good food source, would not always find these mammals the following day. In addition, information on the movements of these birds suggests that a group tends to stay in a certain area (see section under movements). However, according to Ward and Zahavi (1973) there is a correlation between roosting habit and feeding dispersion. Species which feed in flocks upon an unevenly distributed food supply (as in the case of the oxpecker), tend to roost communally. Such flocks feed by "local enhancement" whereby an individual or group seeking food in a particular area quickly determines the location of a good feeding station by seeking a flock that is already feeding, helped in this by the noise or visual conspicuousness of the feeding flock.

As long as a flock is finding food it remains in one place, and is joined by other individuals, but as soon as the local supply of food has been exhausted the flock moves elsewhere, or disbands as its members fly off in various directions to join other flocks they can see or hear. This type of foraging is presumed to be very efficient for the exploitation of patchy food supplies, and is essentially an information-sharing procedure. The information (that here is a good feeding place) is obtained from the finders by other birds in the neighbourhood, the finders for their part assisting the process by advertising their find. Such flock-feeding birds assemble in communal roosts because they need information at two levels. The flock-feeding method only allows the transfer of information within a relatively small area, namely between flocks or individuals which are close together, or come within sight or earshot of one another. However, should the area in question be denuded of food by the birds, or the food sources in it disappear for some other reason, the birds can quickly determine the whereabouts of a new feeding area by taking advantage of the information available in the communal roost which they have been attending regularly. This could be the case in the oxpecker because it was frequently observed that one group of birds feeding on their mammalian symbionts, attracts another group flying overhead.

As suggested by Siegfried (1971b) a species' preference for roosting communally could be an adaptation that has evolved as an energy-saving feature. This is also suggested by Brenner (1965) in the case of the European starling (*Sturnus vulgaris*). Van Someren (1951) observed that at roosting time oxpeckers pile in on top of one another like starlings "going to roost in England". Although the cold weather coincides with a low food supply, there is no direct evidence to support this hypothesis in the case of the oxpecker. As reasoned by Thompson and Coutlee (1963) the whole advantage of social roosting cannot be explained only in terms of energy conservation or protection from predators. According to these authors, the social behaviour of the birds at the roost suggest "that the proximal stimuli are largely social and are not concerned entirely with finding a warm place for the night".

Dowsett (1968) reported that *B. africanus* and *B. erythrorhynchus* occasionally roost on their mammalian symbionts at night in Zambia. He found that buffalo are especially favoured, and giraffe, kudu, eland and black rhino are also recorded as nocturnal hosts. Although several nights were spent searching for oxpeckers on their mammalian symbionts, this behaviour was not observed in the Kruger National Park. Furthermore, all the birds observed in the late afternoon, left the symbionts before nightfall. None of the staff members doing culling operations at night, had seen oxpeckers or heard them on mammals in the Kruger Park. The phenomenon that oxpeckers were only observed on their mammalian symbionts at night in certain areas was also found by Dowsett (1968) and he suggests that roosting on symbionts at night might be expected to be more common in areas where symbionts are sparse. He speculated that it might be more to the advantage of oxpeckers to stay with a wide ranging species during the night, rather than go to roost and then have to search for the symbionts the following day. He also suggested that this was a recently acquired habit.

Defaecation

The red-billed oxpecker was never observed to defaecate on their mammalian symbionts. When defaecating whilst on the symbiont, the oxpecker would lower its body, lift the tail slightly, move backwards and defaecate away from the symbiont. It was observed that birds flying from one symbiont to another, would defaecate in the air.

Intention movements

The flight-intention movement was often observed in the oxpecker. The bird merely crouches, droops the wings a little and points the bill in the direction of intended departure.

Avoidence behaviour

If an observer was too close to a group of symbionts the birds would move to the far side of the mammals or would fly to symbionts farther away.

Predation of adult birds

No records of predation of adult birds were found in the literature and according to Van Someren (1951), oxpeckers do not seem to have any predators in the adult stage. During the study period only three unsuccessful attempts of avian predation were observed. These avian predators were the little sparrowhawk (Accipiter minullus), little banded goshawk (Accipiter badius) and the gabar goshawk (Micronisus gabar). During a predation attempt the oxpecker immediately gave the high intensity alarm call which warned other birds present. Descriptions of the vocalisations of the red-billed oxpecker are given elsewhere (Stutterheim in prep.). The following anti-predatory behaviour was observed:

a) The birds immediately moved to a position between the mammal's fore and hind legs and stayed there until the danger had passed. In that case the mammalian symbiont was used for protection. If intolerance behaviour was shown by the mammalian symbiont, the birds would fly low over the ground to another symbiont.

b) The birds would leave the symbionts and fly into the nearest bush and stay there until the danger had passed.

c) The birds would leave the symbionts and fly away. The pattern of leaving the symbionts differs considerably from the usual flight because the birds would fly low over the ground for a considerable distance before gaining any height. If an avian predator was in hot pursuit, the birds would seek the safety of the nearest bush or symbiont.

Although only a few attempts at predation were observed, the oxpecker also reacted in the presence of the following birds:

White-backed Vulture (Gyps africanus)
Martial Eagle (Polemaëtus bellicosus)
Wahlberg's Eagle (Aquila wahlbergi)
Bateleur (Terathopius ecaudatus)
Lizard Buzzard (Kaupifalco monnogrammicus)
Banded Harrier-hawk (Polyboroides typus)
Yellow-billed Kite (Milvus eagyptius)
Pearl-spotted Owlet (Glaucidium perlatum)

According to Brown (1970) the white-backed vulture, yellow-billed kite, and pearl-spotted owlet are not predators of oxpeckers. It can therefore be speculated that the birds react accordingly as a result of an inherited response to a "hawk shape". According to Manning (1967) there is evidence that wild birds do possess an innate releasing mechanism which enables them to respond to birds of prey on the first occasion that they see them and that they go on responding to birds of prey although few will ever have been attacked. With only three attempts of avian predation observed during the study period, it appears that diurnal avian predation is not an important limiting factor in the ecology of the adult oxpeckers in the Kruger National Park. No other form of predation other than avian predation was observed, in adult birds.

Activity

Feeding

By using the instantaneous and scan sampling method (Altmann 1974) on 12 different mammalian species in the period July 1973 - December 1974, the mean diurnal time budget for feeding was calculated as 68% from a total of 1944 observations (Table 12). It must be borne in mind that these data were collected in all the seasons of the year and that a seasonal variations in feeding behaviour could have had an effect on the accuracy of the calculated data. Furthermore, no adjustment was made for the change in the diurnal period in the different seasons of the year. In an activity study on the oxpeckers on roan antelope during October 1974, the mean diurnal time budget of individual birds for feeding was calculated as 82%. In a statistical analysis it was found that these two mean diurnal time budgets for feeding differ significantly (t-test, $P < 0,05$). The reason for this could be that during the activity study on the roan antelope in October, the birds did not arrive before 09h20. No account can be given of their activity before they settled on the roan antelope.

Table 12 shows the activity preferences of oxpeckers on 11 different mammalian species in the Kruger National Park. A one-way analysis of variance showed that there was a significant difference ($F0,05 > 1,83$) in the feeding behaviour of the oxpeckers on the 11 different mammal species. It can be postulated that the diurnal time budget for feeding is not the same on all the mammalian symbionts or that the oxpeckers do not utilise the different mammalian symbionts to the same extent for feeding. This is probably related to the food available on the different mammalian symbionts and the intolerence behaviour of the different mammalian species (Stutterheim in prep.). Innate intolerance is likely to be a reason for oxpeckers inattention to some mammalian species. When oxpeckers are active on a symbiont, they frequently induce reactions from the symbiont indicative of mild irritation or with the apparent object of dislodging the bird.

Table 12 : Activity preferences of the red-billed oxpecker on different mammalian species in the Kruger National Park obtained in the period July 1973 - December 1974 by using the instantaneous and scan sampling method.

Species of mammal	Activity of oxpeckers					
	% Resting	% Feeding	% Sun bathing	% Feeding young	% Comfort movements	Total number observed activities
Wildebeest	45	14	0	0	40	42
Warthog	26	47	4	0	21	23
Zebra	44	35	2	2	17	149
Eland	32	63	0	0	5	104
Giraffe	7	85	0	1	7	279
Roan	20	73	0	0	7	229
Buffalo	43	35	0	2	20	73
Kudu	18	71	0	0	11	147
Rhinoceros	45	25	3	0	27	98
Impala	18	73	1	0	8	585
Sable	17	75	1	0	7	196
Range	7-45	14-85	0-4	0-2	5-40	
$\bar{x}$	29	54	1	0	16	

All cause the bird to move away from the lender spot or to fly to another symbiont. The reaction of the symbiont to the bird's attentions usually varies with the species of symbiont and the activity of the oxpecker. Feeding appears to be the highest on the eland, giraffe, roan antelope, kudu, impala and sable antelope which are all fairly tolerant animals with a high food load. Furthermore, the feeding behaviour of the oxpeckers appears to be much lower on wildebeest, zebra and warthog which are intolerant animals with a low food load. The utilisation of buffalo and rhino for feeding is also fairly low. The reason for this could be that these animals are tolerant towards the bird but have a low food load.

Table 13 shows the feeding activity of the oxpeckers as related to time of day, on 12 different mammalian species obtained in the period July 1973 to December 1974 and indicates morning and late afternoon feeding peaks. As Ixodid ticks form the main food supply of the red-billed oxpecker (Moreau 1933; Van Someren 1951 and Stutterheim in prep.), it can be speculated that the availability of the food of oxpeckers remains constant throughout the day. This decline in feeding activity can thus probably be linked to the digestion and absorption rate of the food. This follows the general feeding pattern found in the white-crowned sparrow (Zonotrichia leucophrys) (Morton 1967) and red-winged blackbirds (Hintz and Dyer 1970). According to Hintz and Dyer (1970) the early morning feeding behaviour served to replenish food reserves depleted during the night and the late afternoon peak could be related to the rebuilding of energy reserves in preparation for the night. In the activity study on oxpeckers on roan antelope during October, however, mid-day and late afternoon feeding peaks were found (Fig. 7). The reason for this is not known.

The relationship between ambient temperature and the feeding activity of the oxpeckers on 12 different mammalian species obtained in the period July 1973 to December 1974,

Table 13 : General activity of the red-billed oxpecker on 12 different mammalian species in the Kruger National Park as related to time of day and obtained in the period July 1973 - December 1974 by using the instantaneous and scan sampling method.

	Activity of the oxpeckers					
Time of day	% Resting	% Feeding	% Sun bathing	% Feeding of young	% Comfort movements	n
0500 - 0600	0	100	0	0	0	47
0600 - 0700	0	75	0	0	25	30
0700 - 0800	29	53	0	0	18	38
0800 - 0900	23	68	1	0	8	154
0900 - 1000	23	69	0	0	8	220
1000 - 1100	29	61	1	0	9	263
1100 - 1200	29	53	1	0	17	201
1200 - 1300	30	62	0	0	8	169
1300 - 1400	17	67	1	0	15	122
1400 - 1500	22	62	1	1	14	221
1500 - 1600	22	66	1	1	10	228
1600 - 1700	16	77	0	1	6	203
1700 - 1800	14	79	0	0	7	48
$\bar{x}$	20	68	0,5	0,5	10	
Range	0-30	53-100	0-1	0-1	0-25	

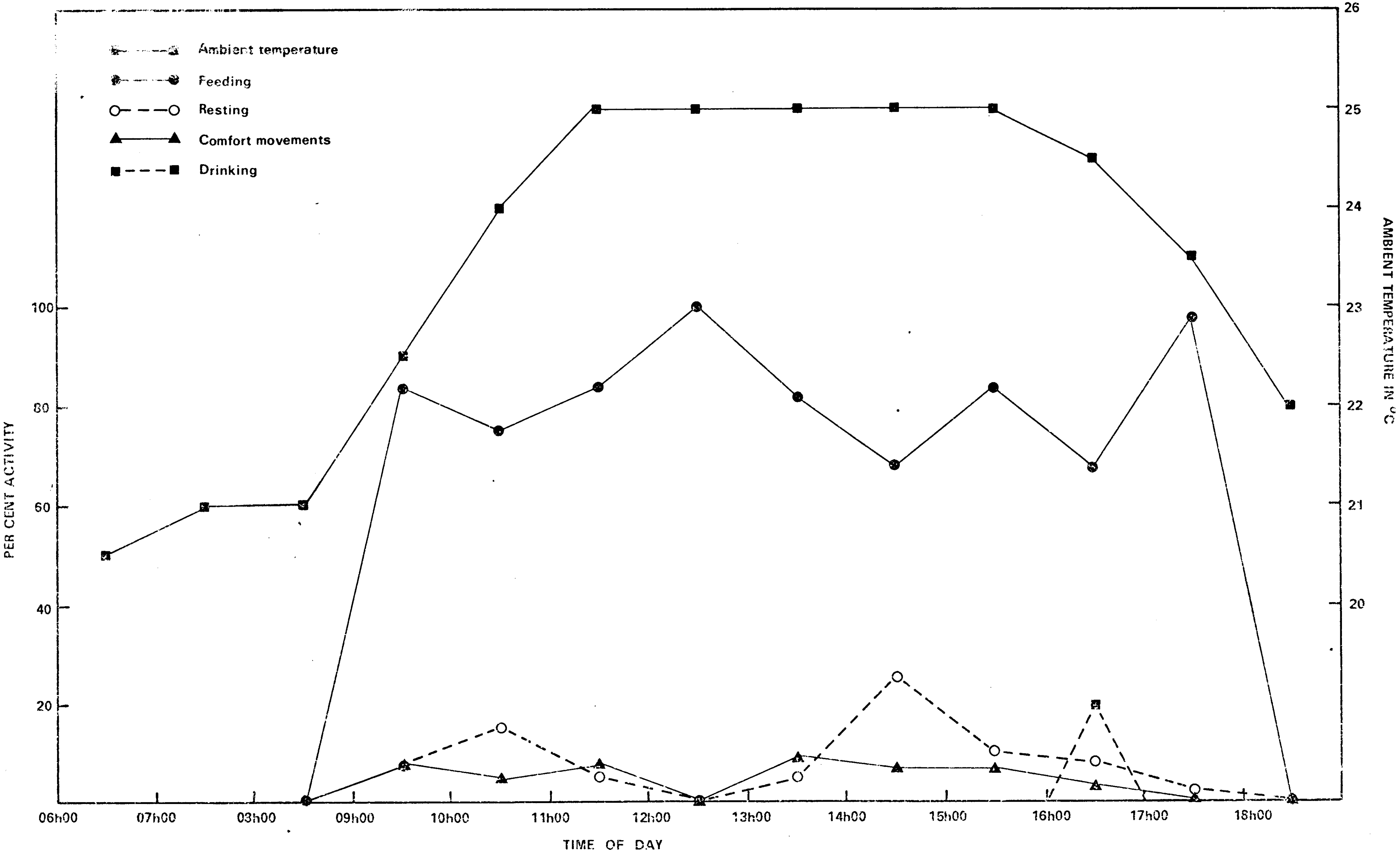


Fig. 7. Activity of the red-billed oxpecker on a group of roan antelope at Nwashitsumbe during October 1974

is given in Table 14. These data were analysed statistically and a test on the coefficient of correlation between the different variables showed that there is no significant relationship (t-test, $P > 0,05$) between the feeding activity of the oxpeckers and ambient temperature. The relationship between the feeding activity of individual oxpeckers on roan antelope during October 1974 and ambient temperature is given in Fig. 7. These data were also analysed statistically and no significant relationship (t-test, $P > 0,05$) was found. It can thus be concluded that there is no relationship between the feeding activity of oxpeckers and ambient temperature. Although no correlation was found, the optimum feeding temperatures of oxpeckers appears to be between 23° C and 29° C (see section under thermoregulatory behaviour).

Verbeeck (1972) has found in the case of the yellow-billed magpie (Pica nuttalli), that feeding occupies a large part of the day but the distribution of time spent on this activity throughout the day varies from month to month, depending on such factors as temperature and priority given to other types of activity. He also states that during the coldest months, the birds spend more time on feeding in the afternoon than in the morning, while the reverse is true during the summer. In the activity study of oxpeckers on roan antelope in October (which is summer in the Kruger National Park), from a total of 501 activities, 23% of the time in the morning and 38% of the time in the afternoon were devoted to feeding. This do not correspond with the findings of Verbeeck (1972) on the yellow-billed magpie. However, the birds settled on the roan antelope at 09h20 and could have been feeding on other symbionts before flying to the roan. A monthly activity study will probably reveal a seasonal change in the feeding behaviour of the oxpecker.

Resting

As it was not always possible to see whether a bird was sitting, perching or thermoregulating, these three activities were combined in the analysis under resting. In

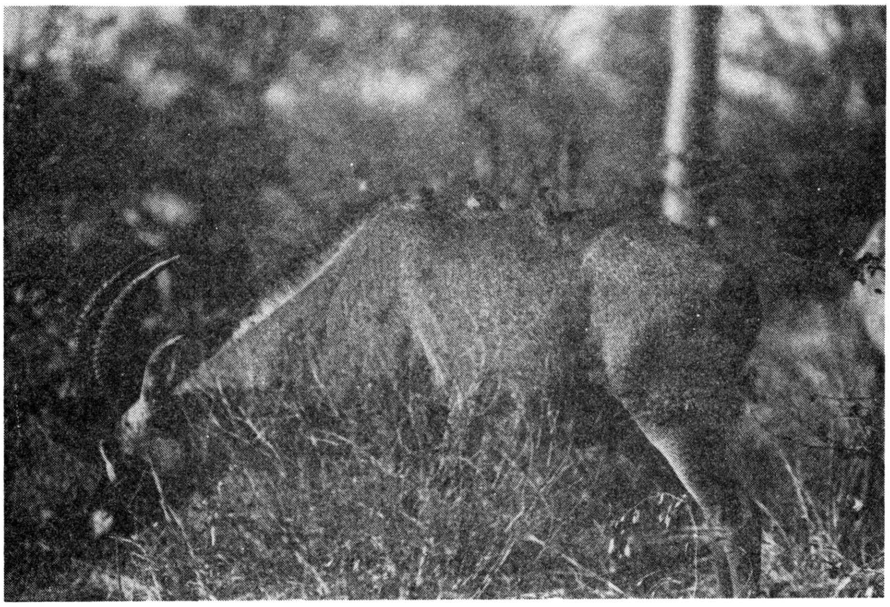
Table 14 : General activity of the red-billed oxpecker as related to ambient temperature in the Kruger National Park obtained in the period July 1973 - December 1974.

Ambient Temperature in ^{o}C	Activity of the oxpeckers					
	% Resting	% Feeding	% Sun bathing	% Feeding of young	% Comfort movements	n
16	47	53	0	0	0	5
17	50	38	0	0	12	8
18	40	60	0	0	0	8
19	22	54	0	0	22	5
20	48	41	0	0	11	16
21	30	49	0	0	21	42
22	42	53	2	0	3	19
23	27	72	0	0	1	29
24	25	65	1	0	9	31
25	34	61	0	0	5	31
26	21	73	1	0	5	35
27	21	69	0	0	10	66
28	39	56	0	0	5	38
29	9	85	1	1	4	69
30	17	74	1	0	8	71
31	19	69	0	0	12	97
32	24	63	0	0	13	100
33	20	60	0	0	20	116
34	18	69	0	0	13	67
35	16	68	0	0	15	83
36	20	68	2	0	10	34
37	35	44	0	4	15	11
38	15	65	0	8	11	19
39	42	50	0	6	2	29
40	20	80	0	0	0	5
ange 16-40	9-50	38-85	0-2	0-8	0-22	

the activity study on the red-billed oxpecker on 12 different mammalian species in the period July 1973 to December 1974, the mean diurnal time budget for resting was calculated as 20% (Table 13). However, in the activity study on oxpeckers on roan antelope during October 1974, the mean diurnal time budget for resting was calculated as 8% (Plate 9). In a statistical analysis it was found that these two mean time budgets for resting differ significantly (t-test, $P < 0,05$). Table 12 shows the activity preferences of oxpeckers on 11 different mammalian species in the Kruger National Park. A one-way analysis of variance showed that there was a significant difference ($F0,05 > 1,83$) in the resting behaviour of the oxpeckers on the 11 different mammalian species. It can thus be concluded that the oxpeckers do not utilise the different mammalian symbionts to the same extent for resting. This is probably related to the intolerance behaviour of the mammalian symbiont and ambient temperature (see section under thermoregulatory behaviour). Resting is the highest on wildebeest, zebra, buffalo and the white rhinoceros. It is not clear why resting is an important time expenditure on zebra and wildebeest because they are fairly intolerant animals (Stutterheim in prep.). It could be, however, that the birds are tolerated by these mammals if they remain quiescent on the back of the symbiont but are not tolerated once they start feeding.

Table 14 shows the relationship between resting and ambient temperature. These data were analysed statistically and a test on the coefficient of correlation between the variables showed that there is a significant relationship (t-test, $P < 0,05$) between the resting activity of the oxpeckers and ambient temperature. However, with a negative correlation ($rs = -0,5$), it can be postulated that with an increase in ambient temperature, there is a decrease in resting behaviour. Furthermore, although a significant correlation was found between the resting behaviour of the oxpeckers and ambient temperature, resting appears to be

Plate 9. A red-billed oxpecker resting on the back of a roan antelope at Nwashitsumbe, October 1974.



maximum at low and high ambient temperatures. The reason for this is unknown, but it is probably related to thermoregulatory behaviour (see section under thermoregulatory behaviour).

A significant correlation (t-test, $P < 0,05$) was also found between the resting and feeding activities of the oxpeckers (Table 13). As resting and feeding are the most frequently observed activities in the oxpecker, an increase in the feeding behaviour will correspond with a decrease in resting behaviour and vice versa. The same was found in the activity study of the birds on roan antelope in October 1974 - a peak in feeding is usually followed by a peak in resting (Fig. 7). Furthermore, with an early morning and late afternoon feeding peak, resting was not observed before 07h00 and appears to decrease after 15h00. The general activity study of the oxpecker on 12 different mammalian species in the period July 1973 to December 1974, indicates a maximum resting period between 11h00 and 13h00. However, this was not found in the birds feeding on roan antelope in October 1974 as shown by Fig. 7. The reason for this is not known.

Comfort movements

Comfort movements include all the behaviour concerned with the care and comfort of the body. In the activity study on the red-billed oxpecker, the term comfort movements included stretching, scratching, bill-cleaning, preening, chin-rubbing and dust-bathing. Although sleeping is usually associated with comfort movements, it was classified in the activity study under the term resting. In the activity study on the oxpecker on 12 different mammalian species in the period July 1973 to December 1974, it was calculated that 10% of the diurnal time budget is devoted to comfort movements (Table 13). In the activity study on the oxpeckers on roan antelope during October 1974, the mean diurnal time budget for comfort movements was found to be 5,4%. These two calculated mean time budgets for comfort movements were analysed statistically and no significant difference (t-test, P > 0,05) was found between the results of the two sets of data.

Table 12 shows the calculated time budgets for comfort movements of the oxpeckers on 11 different mammalian symbionts. A one-way analysis of variance showed that there was a significant difference (F0,05 > 1,83) in the diurnal time budget of the oxpeckers for comfort movements on the 11 different mammalian symbionts. It can thus be concluded that the oxpeckers do not utilise the different mammalian symbionts to the same extent for comfort movements (see section under the activity of oxpeckers as related to their mammalian symbionts). Comfort movements appear to be the highest on the wildebeest, zebra, warthog, buffalo and white rhinoceros. Moreover, comfort movements were less frequently observed on eland, giraffe, roan, impala and sable antelope. This is probably related to the intolerance behaviour of the mammalian symbiont and ambient temperature (see section under thermoregulatory behaviour and Stutterheim in prep.).

Table 14 gives the relationship of ambient temperature and the comfort movements of the oxpeckers. In an analysis of the coefficient of correlation, no significant relationship (t-test, P> 0,05) was found between the comfort movements of the oxpeckers and ambient temperature. However, from the results obtained from the activity study of the oxpeckers on 12 different mammalian species in the period July 1973 to December 1974, there appear to be an early morning and early afternoon peak in comfort movements. Further, the early morning peak in comfort movements followed the early morning feeding peak and the afternoon peak in comfort movements followed the midday peak in resting behaviour. However, no significant correlation (t-test, P> 0,05) was found between the comfort movements of the oxpeckers and resting and feeding behaviour. (Figs. 8 and 9).

According to Verbeeck (1972) preening is associated with moult. Timing of moult is adaptive in that it occurs at a time when high ambient temperatures require less time

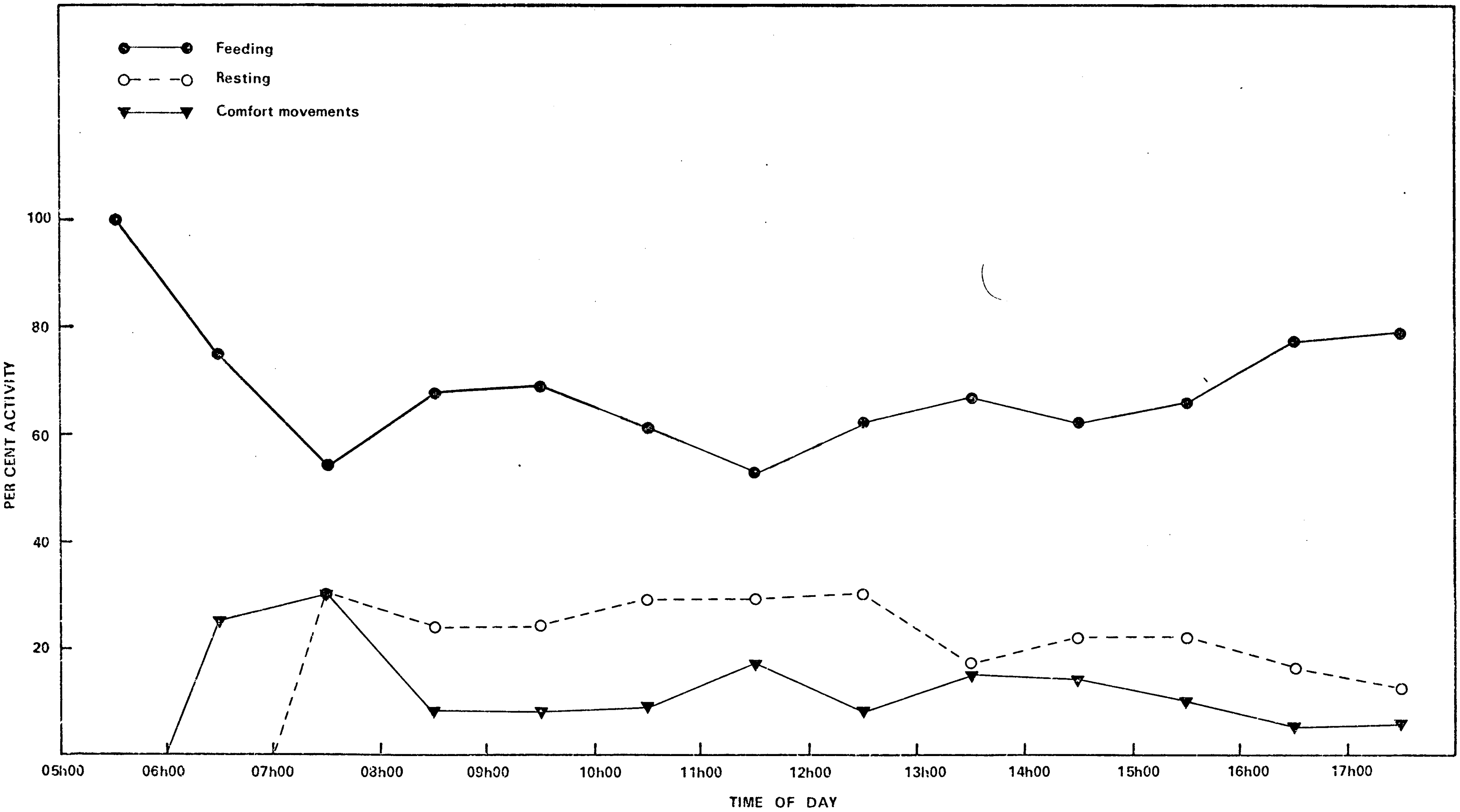


Fig. 8. General activity pattern of the red-billed oxpecker om 12 different mammalian species as recorded from March 1973 until December 1974 in the Kruger National Park

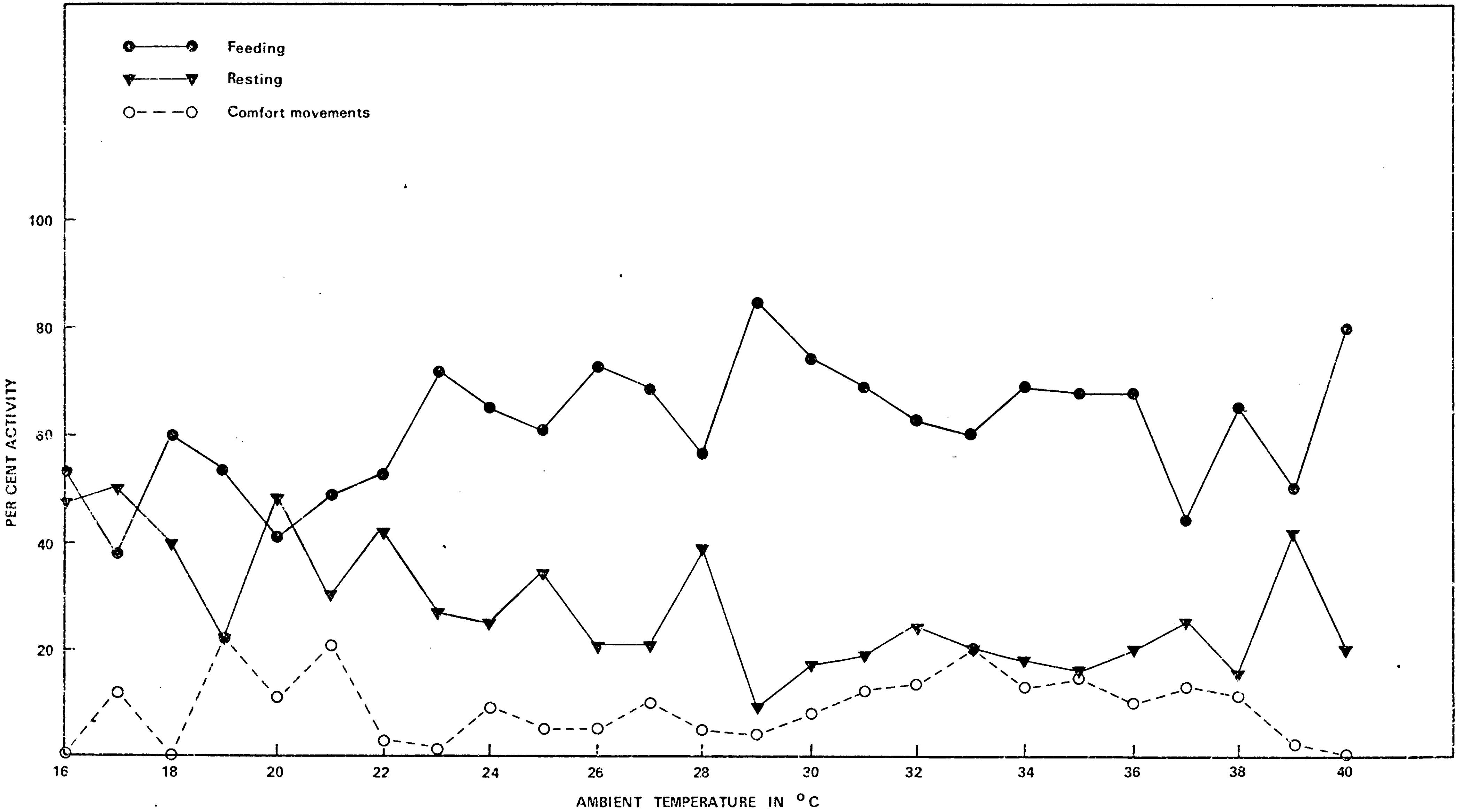


Fig. 9. General activity of the red-billed oxpecker as related to ambient temperature on 12 different mammalian species in the Kruger National Park as recorded from March 1973 until December 1974.

for procurement of food, which in turn allows more time for resting and preening. In the Kruger National Park, the red-billed oxpecker has two moult cycles annually - a partial moult cycle with the beginning of the rainy season and a complete moult cycle after the breeding cycle (see section under the moult cycle). As preening is the most frequently observed comfort movement in the oxpecker, a seasonal variation in comfort movements probably does occur. A montly activity study will probably reveal this seasonal change.

Table 13 shows the comfort movements of the oxpeckers on 12 different mammalian symbionts in the Kruger National Park as related to the time of day and obtained in the period July 1973 to December 1974. Although no adjustment was made for the change in the diurnal period in the different seasons of the year, it was calculated that 59% of the comfort movements were observed between 05h00 and 12h00. In a statistical analysis a significant difference (t-test, $P < 0,05$) was found between the percentage comfort movements observed in the morning and afternoon with comfort movements the highest in the morning (05h00 - 12h00).

Activity of oxpeckers as related to their mammalian symbionts

In the Kruger National Park, oxpeckers utilise 15 different mammalian species. These mammalian species differ in size, shape, behaviour and habitat preferences. It can also be postulated that each species has its own optimum time budget that is adapted to local environmental conditions.

By using the instantaneous and scan sampling method, the activity preferences of oxpeckers on 11 different mammalian species in the Kruger National Park were obtained in the period July 1973 to December 1974. A one-way analysis of variance showed that there was a significant difference ($F0,05 > 1,83$) in the feeding behaviour, resting behaviour and comfort movements of the oxpeckers on these different mammalian symbionts.

Although some of these mammal species are extensively utilised, individual birds do not stay on the same species all the time. It can thus be postulated that oxpeckers will favour a specific mammal species or individual symbiont that could fulfil the maximum needs for a particular activity. This behaviour was most prominent in the case of the white rhino in a camp near Pretoriuskop. These rhino had a morning and afternoon feeding peak with a midday siesta. The oxpeckers left these mammals soon after the start of the morning feeding period but again returned during the resting period. This behaviour is related to temperature because the rhino usually fed in the sun and rested in the shade (see section under thermoregulatory behaviour). This also explains the high percentage of resting (45%) and comfort movements (27%) on the white rhinoceros. These rhino were never observed drinking water during the daytime period with the result that the oxpeckers had to leave them to drink. The white rhino is also a very tolerant symbiont and is thus favoured as a resting platform (Stutterheim in prep.).

From Table 12 it appears that oxpeckers prefer certain mammalian species for feeding and others for resting and comfort movements. This can probably be related to the activity of the symbionts, intolerance behaviour of the symbionts and food load found on the symbionts (Stutterheim in prep.). A good example is the wildebeest (Connechaetes taurinus). The wildebeest has a very low relationship with oxpeckers of 0,02 birds per animal and a high intolerance behaviour towards the birds. The wildebeest is mainly utilised near water if no other symbionts are present, as a perch for drinking purposes and for preening after a bath. Although some feeding was observed, the wildebeest is mainly utilised when standing in the shade during the midday heat as a resting perch. This behaviour on the wildebeest is clearly shown in Table 12 by a high occurence of resting (45%) and comfort movements (40%) and a low occurence of feeding (14%).

Figs. 7 and 10 show the relationship between the activity of a group of roan antelope, oxpeckers and the ambient temperature during October. The first bird arrived at 09h20 and the last birds left at 17h50. In an analysis of the coefficient of correlation, no significant correlation (t-test, $P > 0,05$) was found between the activities of the oxpeckers and roan antelope. From Figs. 7 and 10, however, it appears that there is a direct relationship between the drinking behaviour of the oxpeckers and the drinking behaviour of the roan antelope. It must be borne in mind that this was an activity study performed on a group of birds and not on an individual bird. Although some birds drank at the same time as the symbionts, a large number of birds left the symbionts during the day and flew in the direction of the nearest water point. These activities of the birds away from the symbionts were not recorded.

The relationship between the activity of the oxpecker and the activity of the impala, obtained by using the instantaneous and scan sampling method in the period July 1973 to December 1974, is given in Table 15. A two-way analysis of variance indicated a significant difference $(F0,05 > 0,001 < 10,97)$ in the activity of the oxpeckers as correlated with the different activities of the impala. Feeding appears to be the highest on the feeding and standing (resting in the standing position or ruminating) impala and resting appears to be the highest in the walking impala and when they lie down. A "resting" bird on a walking impala, however, could be a perching bird unable to feed. Furthermore, the comfort movements of the oxpecker appear to be the highest on the feeding and standing impala. For some unknown reason, very few comfort movements were observed on impala. From the foregoing it can be concluded that the oxpeckers utilise the different mammalian symbionts for a particular activity or need and this could be related to the activity preferences of the mammalian symbionts at the specific time of day and the intolerance behaviour of the symbiont species.

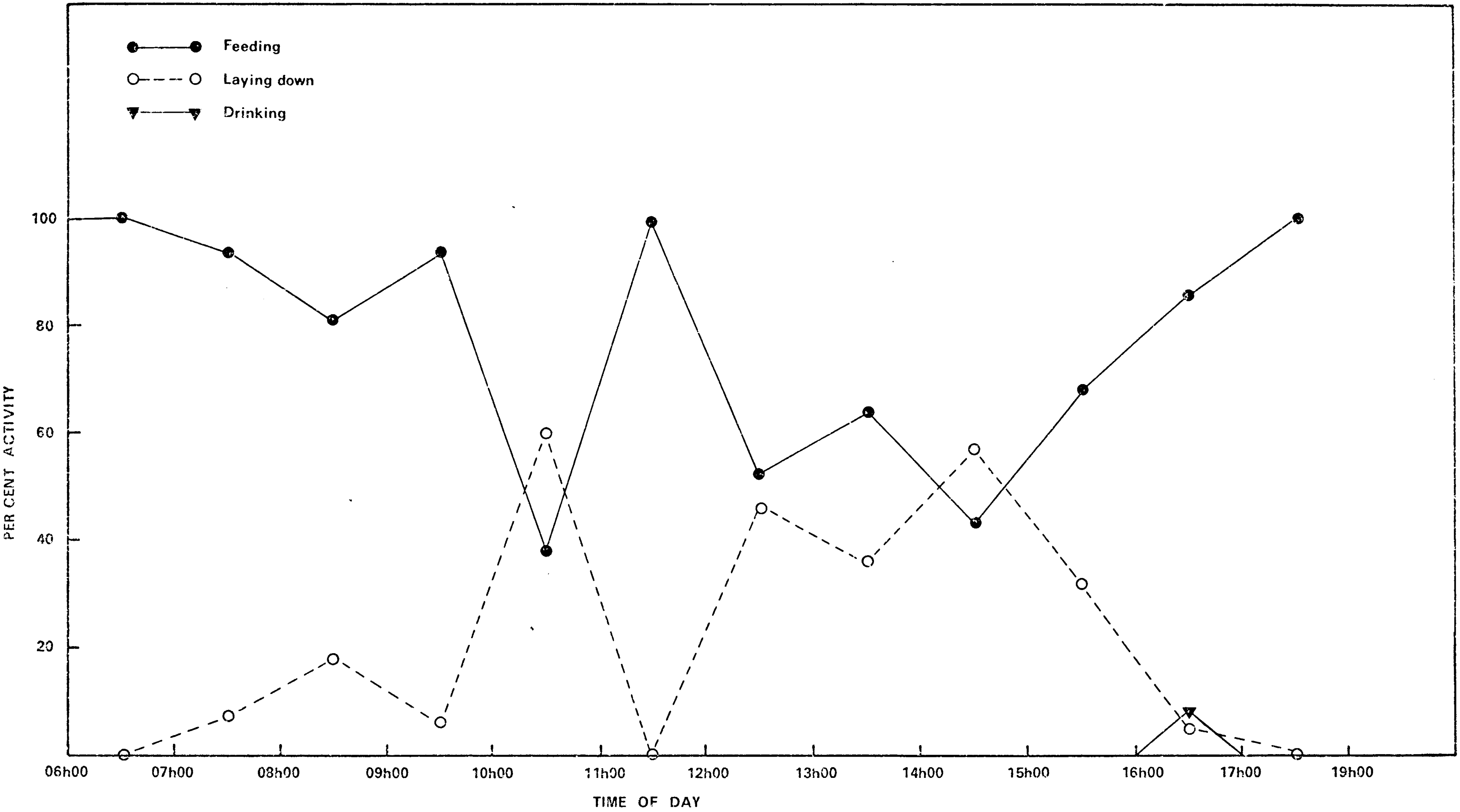


Fig. 10. Activity pattern of a group of roan antelope at Nwashitsumbe during October 1974-

Table 15 : Activity of the red-billed oxpecker as related with the activity of impala in the Kruger National Park obtained in the period July 1973 - December 1974 by using the instantaneous and scan sampling method.

Activity of impala	Activity of the oxpeckers			
	% Resting	% Feeding	Comfort movements	Total number observed activities
Laying down	45	55	0	11
Walking	51	43	5	39
Feeding	17	73	9	128
Standing	17	74	10	385
Range	17-51	43-74	0-10	
$\bar{x}$	33	61	6	

CHAPTER 6

MOVEMENTS

Introduction

Home range size, juvenile dispersal, migration patterns and daily movements all figure importantly in avian ecology. One objective in this study has been to measure red-billed oxpecker population changes and trends in a large area. The area selected was the Skukuza area in the southern part of the Kruger National Park (Fig. 1).

The number of birds in an area at a given time depends upon the amount of reproduction, mortality and movements. Bird ringing, a standard ornithological tool, is of limited value in determining the above because of low recovery rates. It was the need for a method of securing large population samples over a large area in a limited time that led to the selection of a monthly trapping, colour marking and roadside census. However, as trapping was only possible at the animal pens of the Veterinary Division at Skukuza, the term population as used in this paper refers to the total number of individuals of both sexes and all ages (other than nestlings) that visited these pens at Skukuza.

Results

Behaviour responses to the ringing procedure

A bird when netted or handled will display a range of behavioural responses typical of the species (Berruti 1974). When entangled in the nets, the oxpeckers usually gave the alarm call and showed escape orientated behaviour in the form of struggling (Plate 1). Descriptions of the vocalisations of the red-billed oxpecker are given elsewhere (Stutterheim in prep.). When a human approached the nets the struggling increased and stress was indicated by defaecation. Vocalisation was a rattling distress call. Disentangling was often hampered by aggressive pecking by the birds. During the marking process, displacement activities were observed, for instance, of preening, crest erection and scissoring.

All the birds released at the pens immediately settled on the animals, adopted the pengiun attitude (Attwell 1966) and gave the alarm call. This was followed by feather shaking and preening.

The behaviour of oxpeckers in giving a rattling distress call when being handled often attracted other oxpeckers in the immediate vicinity. A few of the attracted birds dived aggressively on the person handling the bird and got themselves entangled in the nets. A tape recording of this rattling distress call could be used to increase trapping success.

Ringing and retrap data

A summary of daily captures, netting hours and recaptures is given in Appendix 1. By using two 20 m nets a trapping success of 1,2 birds per trapping hour was obtained. This gives a total trapping success of 203 birds of which 48 were recaptures in a 250 hour trapping period.

Trapping success appeared to be highest during 10h00 - 12h00 and 14h00 - 17h00 (Table 16). However, disturbances by humans could be the reason for these two peaks. In the Satara area, from the breeding data, the replacement rate of the red-billed oxpecker was calculated as 0,8 chicks per adult for the 1973/74 breeding season and 0,5 chicks per adult for the 1974/75 breeding cycle (see section under breeding behaviour). This gives a mean age ratio of 0,65 fledglings per adult bird. As Satara is 90 km from Skukuza, it can be speculated that the replacement rate would be the same for the Skukuza area. With a high trapping success (41%) for first-year birds, in the Skukuza area it can be postulated that young birds are much easier to trap than adults. Learned avoidence behaviour could be the reason for this.

Figure 11 indicates a big variation in the monthly trapping success. However, the large number of factors that could influence the trapping success must be considered.

Table 16 : Trapping time of the red-billed oxpecker at the animal pens of the Veterinary Division at Skukuza in the period March 1973 - December 1974.

Time	Number birds	Per cent birds of total trapped
06h00 - 07h00	0	0
07h00 - 08h00	0	0
08h00 - 09h00	2	1
09h00 - 10h00	16	8
10h00 - 11h00	24	12
11h00 - 12h00	27	14
12h00 - 13h00	12	6
13h00 - 14h00	20	10
14h00 - 15h00	32	16
15h00 - 16h00	22	11
16h00 - 17h00	28	14
17h00 - 18h00	6	3
18h00 - 19h00	2	1
19h00 - 20h00	3	2
Total	194	
Range	0-32	

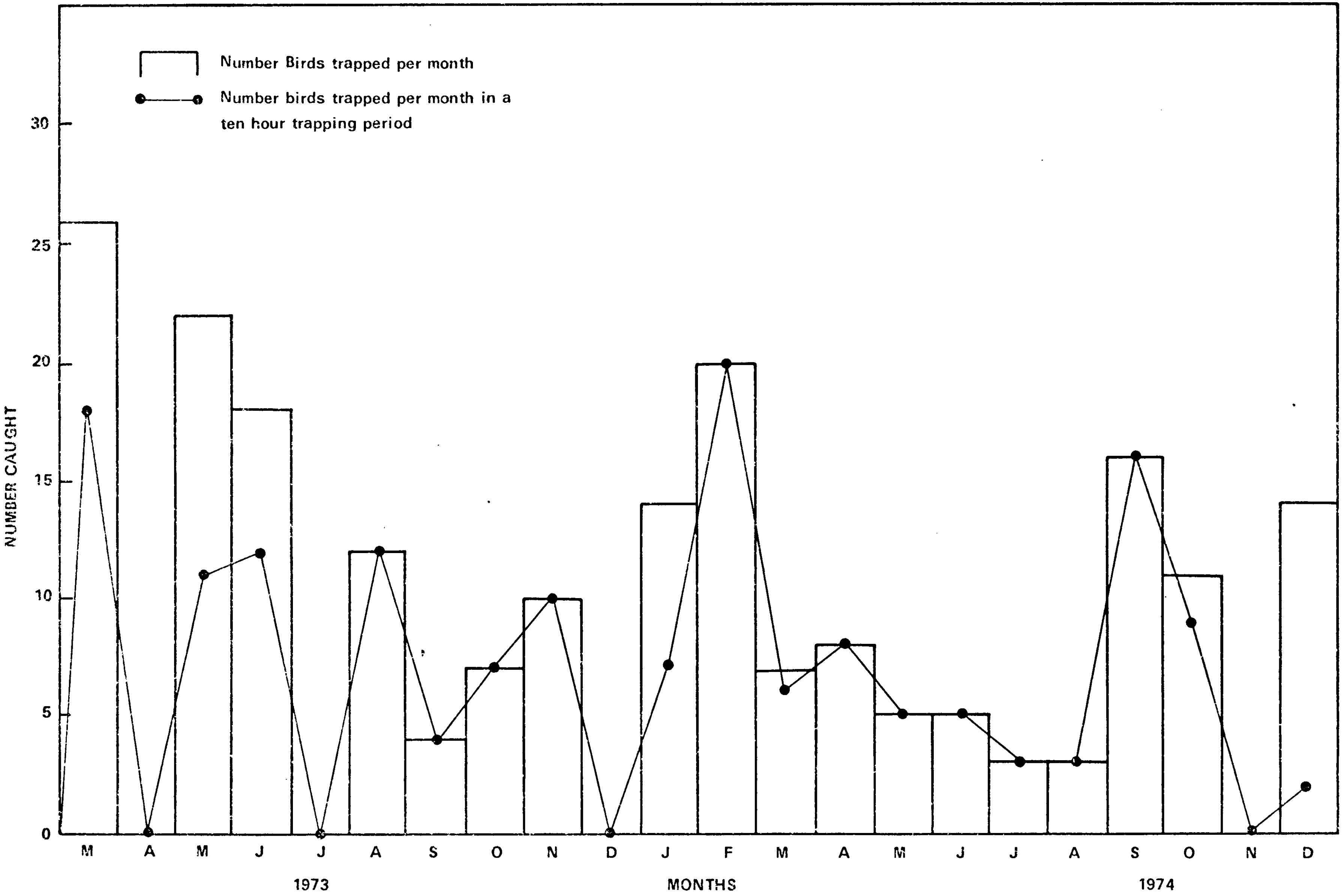


Fig. 11. Number of red-billed oxpeckers caught per month and the number trapped every month per ten hour trapping time at Skukuza during the period March 1973 to December 1974.

In this study the most obvious variations in monthly trapping success are due to net-shyness and disturbances by humans. Figure 12 indicates a steady decrease in the percentage of accumulated new rings to the totals and a steady increase in the percentage of accumulated recaptures to the totals. This points to a resident population of birds that visit the animal pens. Further evidence indicating a stable population is clearly shown in Fig. 13 by a more or less constant increase in number of recaptures.

Net-shyness can be expected to manifest itself in a progressive decline in catch per effort. This is clearly seen in Fig. 11 by a steady decline in trapping success from March until September 1973. According to Stamm _et_ _al_. (1960) an interplay can occur between recruitment and net-shyness. It appears that the only recruitment in the study population is an influx of young birds during the breeding season as seen by an increase in trapping success during the summer months despite an increase in net-shyness.

The mean recapture time in the 19 month trapping period is six months, with a maximum recapture time of 19 months. The frequency of recaptures is summarised in Fig. 15. From a total of 155 birds ringed, 23 were recaptured once, nine recaptured twice, two recaptured three times and one bird recaptured five times. The frequency of the recapture time after the birds were ringed for the first time is summarised in Fig. 14. From a high incidence of one to three months in recapture time, the conclusion can be drawn that the oxpeckers return to the trapping station after being trapped and marked. This emphasises the value of trapping only once a month and using a marking method with a minimum disturbing effect on the birds.

Estimation of the number and mortality of the birds in the study population

The many and diverse schemes for estimation of population numbers are summarised by Giles (1971). If the method of Stamm _et_ _al_. (1960) is used on the basis of recapture it must be based on the following reasoning. If a number of birds are banded and released, then the reciprocal of the

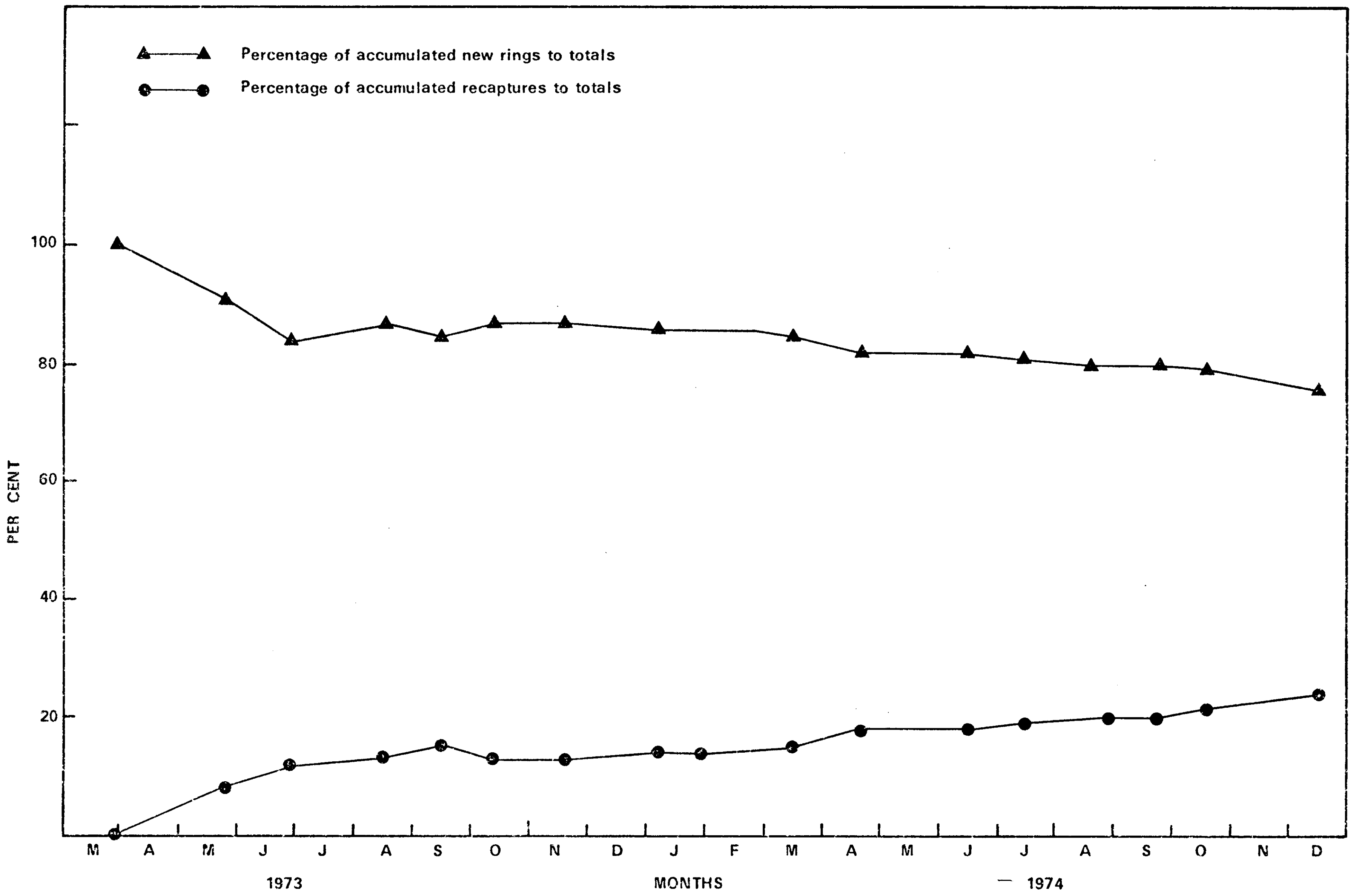


Fig. 12. The relationship between the percentage of accumulated new rings and accumulated recaptures to totals of the red-billed oxpecker in the Skukuza area during the period March 1973 to December 1974.

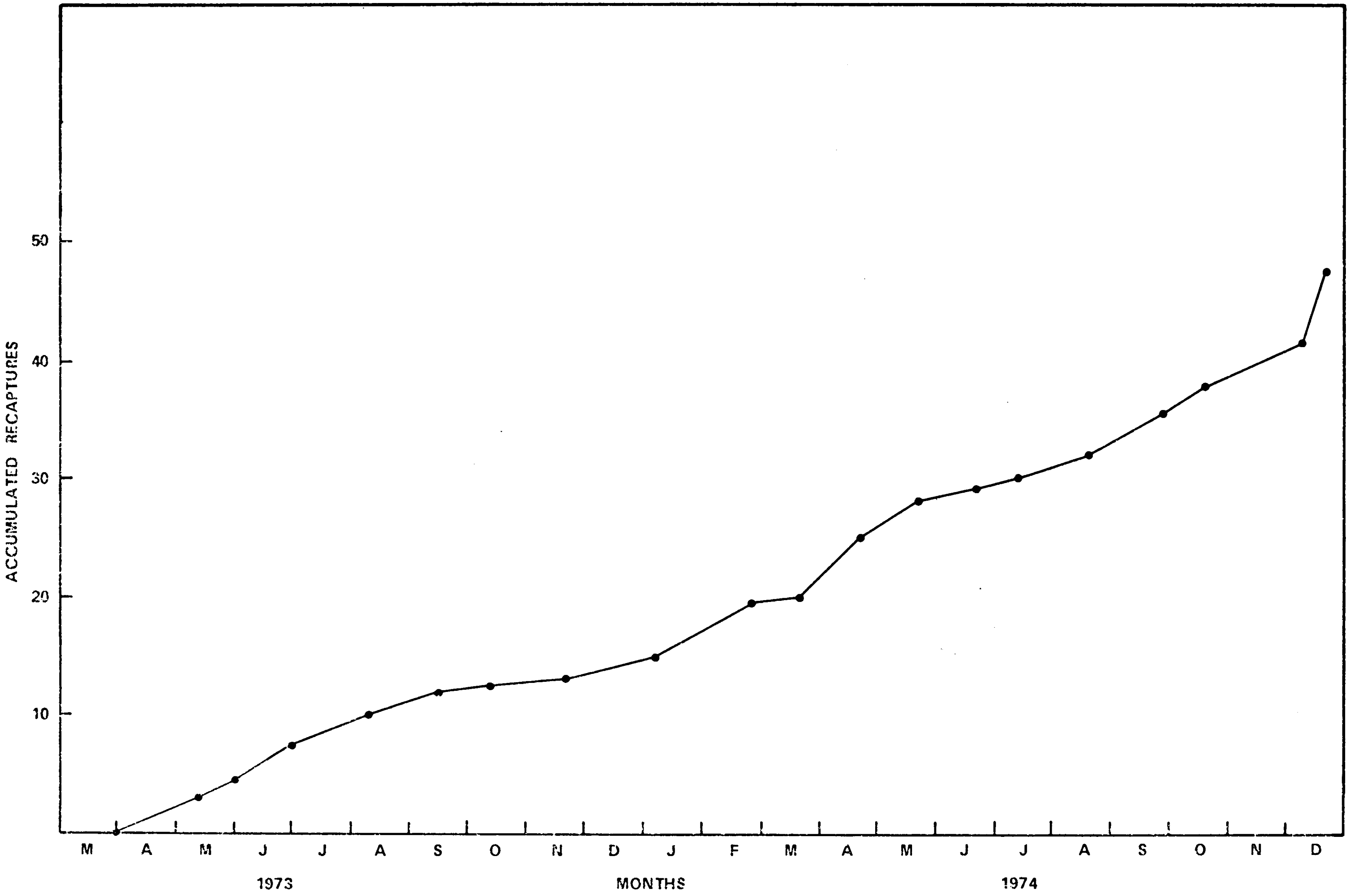


Fig. 13. The accumulation of recaptures in the red-billed oxpecker in the Skukuza area ringed over the period March 1973 to December 1974.

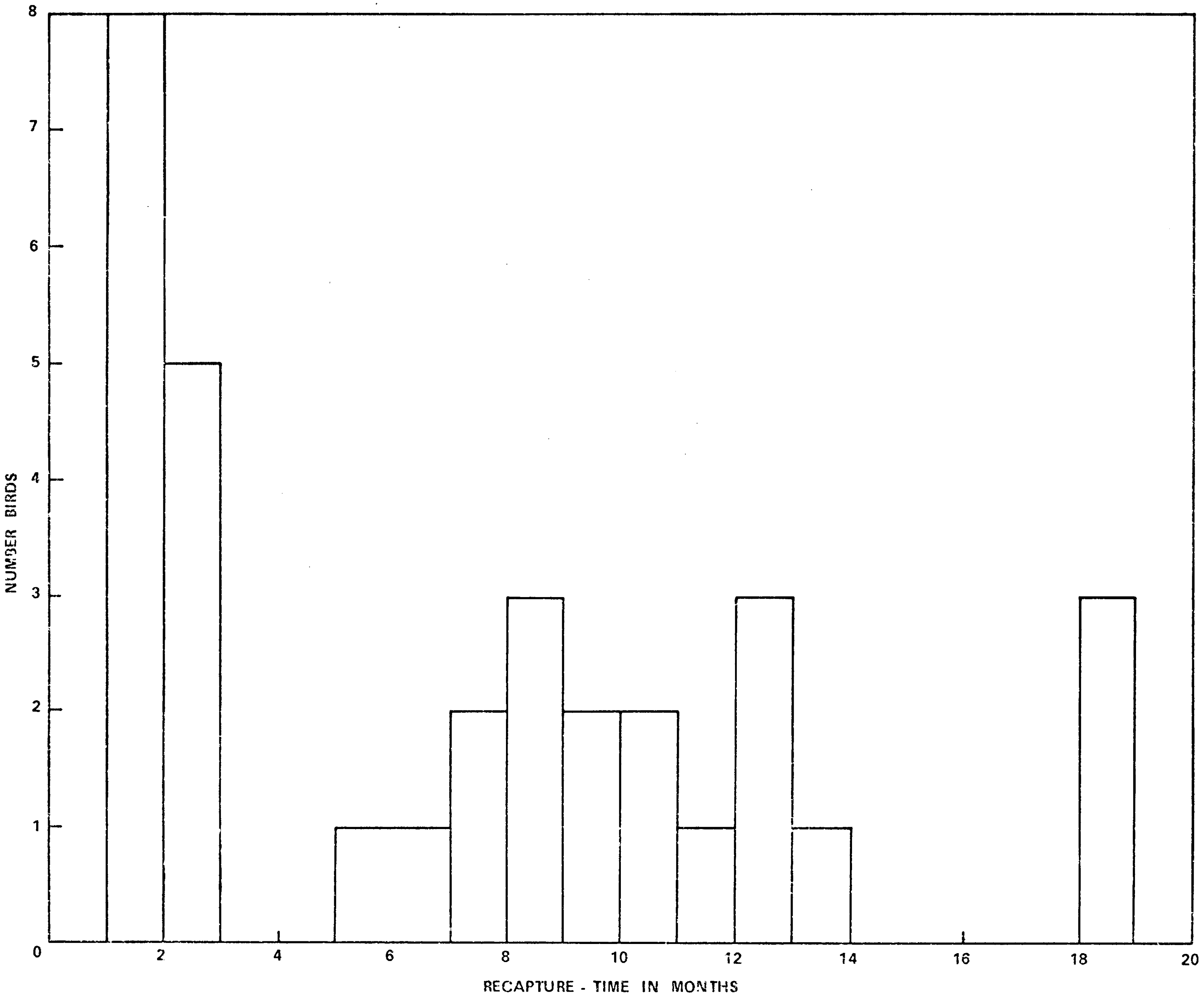


Fig. 14. Recapture - time of the red-billed oxpecker ringed at Skukuza over the period March 1973 to December 1974.

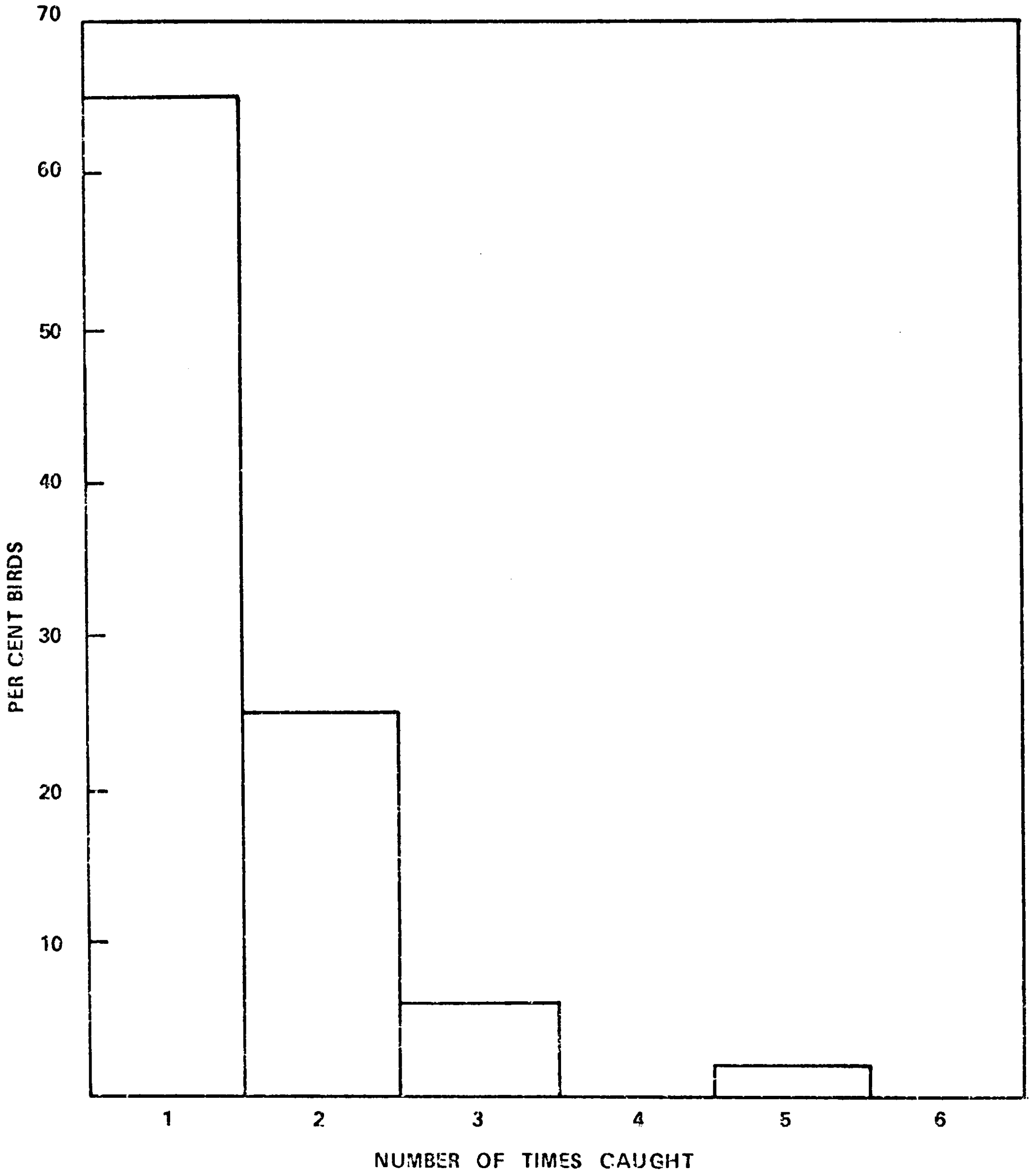


Fig. 15. Frequency of capture of the red-billed oxpecker in the Skukuza area over the period March 1973 to December 1974.

proportion of banded birds in a subsequent sample multiplied by the number marked originally, gives an estimate of the original population. This relationship is expressed in the formula:

$$N = \frac{Mn}{m}$$

N = the estimated number of birds present during the marking period.

M = the number of birds banded and released during the marking period.

n = the total number of birds captured during the sampling period.

m = the number of birds captured during the sampling period that were captured and released banded during the marking period.

The standard error of N is calculated from the formula:

$$S.E. = \sqrt{\frac{(M)^2 \; n(n - m)}{(m)^3}}$$

(Baily 1951, In: Stamm et al. 1960).

Population estimates made by this method are based on the following assumptions:

1. No loss or gain of marks.
2. No difference in mortality of marked and unmarked individuals.
3. Random distribution of marked and unmarked individuals or random sampling.
4. No recruitement, no difference in departures of marked and unmarked.
5. Behaviour and catchability the same in marked and unmarked.

Assumptions one and three are valid for the period of this study or the variations are minimal and therefore unimportant. Eighty three per cent of all the birds marked were marked with colour rings which is a safe and inconspicuous method and it is therefore highly unlikely that it could have had any effect on the mortality rate of the oxpeckers.

However, assumptions four and five are not valid in this study and could have an effect on the estimated number of the study population. Although a few birds were collected in the Skukuza area once a month, these birds were collected in the vicinity of the Renosterkoppies dam (16 km from Skukuza) and could not have effected the population estimate (see section under sightings of marked birds). If the sampling period 10 - 16 December 1974 is used (Appendix 1) the study population (or the number of birds that visited the animal pens at Skukuza), was estimated as 241 birds with a standard error of 48. However, trapping success was influenced by a number of factors which could have influenced this estimate. If the trapping session of every month is taken as the sampling period, the mean population size was estimated as 351 birds. If it is assumed this is the number of oxpeckers which visited the animal pens at Skukuza then it can be calculated that 42% of the study population was marked.

By using this evidence, mortality rate can be calculated by using the method suggested by Davis (1951). During 1973 86 birds were trapped, marked and released. In 1974 104 birds were trapped of which 17 were ringed the previous year. If it is assumed that the proportion of marked birds is the same in the untrapped population then the marked birds in the total population are $\frac{17}{104}$ (351) = 57. Since 87 birds were marked during 1973 the probability of surviving for a year is $\frac{57}{87}$ = 0,6. The probability of dying is therefore 0,4. This postulation can only be correct if no local movements occur in the study population. However, the catchability of marked and unmarked birds is not the same. This could have an effect on the calculation of the mortality rate of the oxpeckers.

Sightings of marked birds

Of the 155 marked birds, 22 or 14% were resighted out of a total of 41 sightings. The frequency of distances travelled by the oxpeckers are indicated in Fig. 16. The

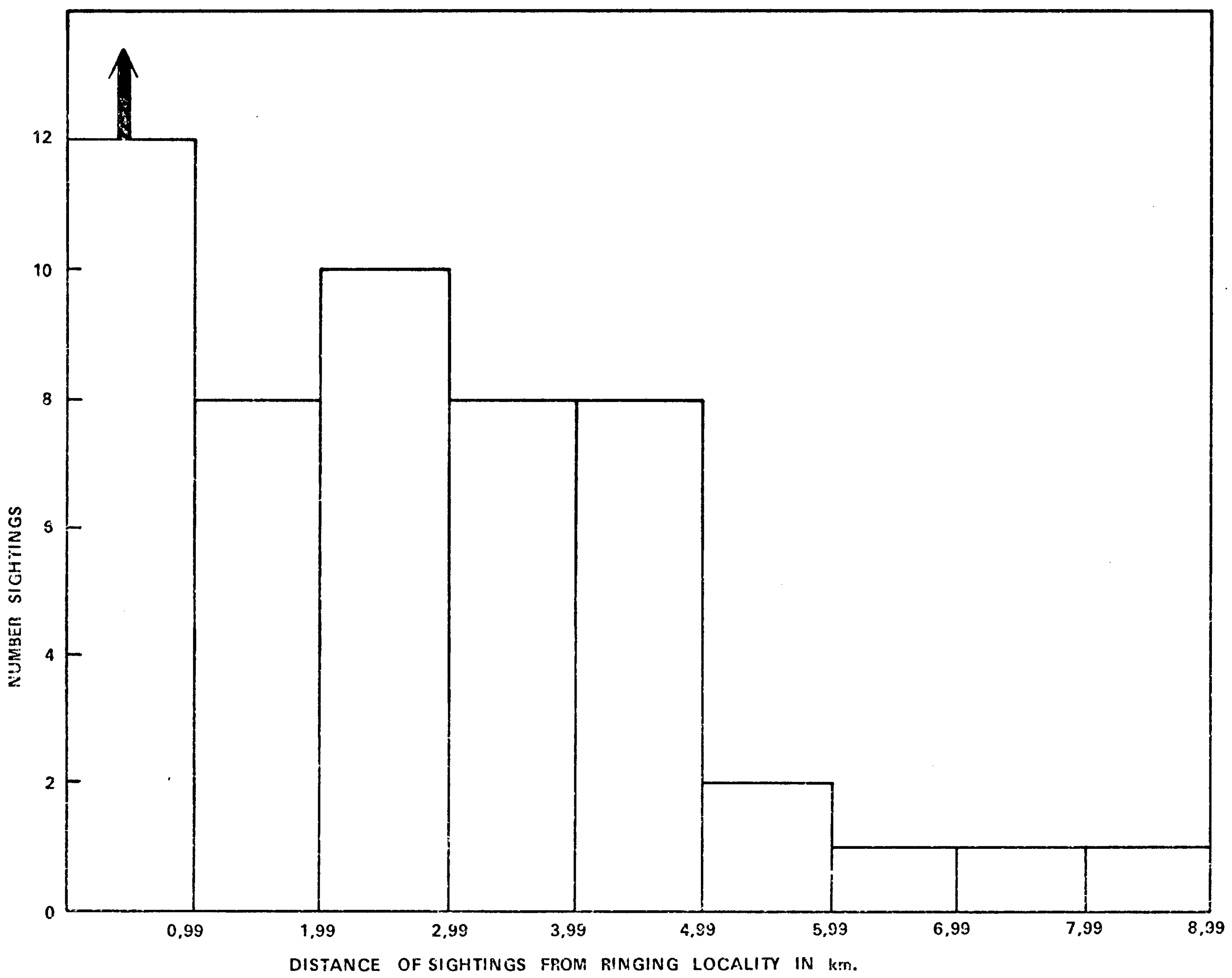


Fig. 16. Distances red-billed oxpeckers were observed from the ringing locality at Skukuza over the period March 1973 to December 1974.

maximum distance the oxpeckers were observed away from the animal pens measured 8,0 km with a mean distance of 3,37 km. If it is assumed that the activity zone of birds is circular and the maximum distance travelled equals the radius of the zone, the activity zone of the study population can be calculated as 198 km^2.

Sightings of marked birds were limited to the area covered by roads. However, sufficient resightings of a marked bird when plotted on a map describe the area over which the bird ranged, hereafter called the "home range". A home range as defined by Pettingill (1970) is the total area that a bird habitually occupies. For most of the marked individuals too few data were obtained from individual birds to delimit a home range. For two birds (five and four resightings respectively) circular home ranges of 26 km^2 and 27 km^2 can be calculated from a maximum distance between resightings of 5,8 and 6,0 km, if this maximum distance is taken as the diameter. The resightings from these two birds indicate that individual birds or groups, tend to feed in certain areas.

A high percentage (42%) of the birds were resighted along the Sabie river. A reason for this could be the high game concentration along the river front or could be a bias originating from the distribution of the roads. No permanent roost was found in the study area so that no account can be given of the daily movements between the roosting area and the feeding area or of any change in roosting area.

Discussion

Williams (1963) refers to the red-billed oxpecker as a partial migrant in East Africa, while Haldane (1951) records the numbers of the yellow-billed oxpecker varying considerably from year to year at Bufagi, Tanzania. An interesting and only reported recovery of the red-billed oxpecker outside the Kruger National Park is a bird shot at the Lukanga river in Zambia which had moved 64 km over a period of 16 months (Elliot & Jarvis 1970). Counts made by Mundy and Cook (in press) at a yellow-billed oxpecker roost in Nigeria indicate a seasonal variation in numbers of birds which points to local movements and/or a change in roosting area. The results obtained from marked red-billed oxpeckers at Skukuza show that the study population has no seasonal fluctuations in numbers, and appears to have little or no local movements. It can thus be concluded that the population during the study period was permanently resident.

During most of the year the birds feed on very mobile mammals which may be widely scattered throughout the area. In addition, the mammals must support varying loads of parasites due both to a species and individual factor and to the local conditions prevailing. As would be expected from the habits of the species, their distribution, movements and abundance are related to the concentrations of their mammalian symbionts which provide their food, although no experimental data exist to prove this statement (Attwell 1966 and Kemp 1972).

The distribution of large mammals in the Kruger National Park has been described by Pienaar (1963, 1966) and Joubert (1973). Although vegetation type is one of the most important factors governing an animals selection of a particular habitat (Dice 1952), water is in many instances equally important, both physiologically and ecologically (Young 1970). Not only does the availability of drinking water limit the density obtained by species in a particular area (Dasman 1964) but should it be absent either temporarily or permanently, water dependant species will to a large extent not be able to utilise the area (Smuts 1972). The study area is transversed by the perennial Sabie river. The grazing strips surrounding the river support a biomass of 36137,6 kg/km^2 of mixed mammalian species during the dry season (Pienaar 1966). Although some of this game moves to more favoured summer grazing areas during the wet season the river front still supports a high summer game concentration, especially impala (Stutterheim in prep.).

The dependance of game on surface water can also be gauged when studying the "cruising radius" or mean daily distance which they move away from a watering point. Young (1970) found the average daily "cruising radius" for impala 1,6 km, buffalo 6,0 km, zebra 3,5 km and wildebeest 2,6 km. These distances are, however, not only determined by the water requirement of the animal, but also by the condition of the veld surrounding the particular waterhole (Van der Schijff 1957, 1959). Distances in excess of eight kilometers usually entail movement from one waterhole to the next, rather than a true "cruising radius" (Smuts 1972). Because of the fact that the Sabie river is a perennial river (at least during the study period) this does not happen along the river front.

It can thus be speculated that the study area supported a high symbiont concentration during both seasons. Hence in whatever direction a bird or a group of birds may travel they will soon encounter sufficient quantities of suitable food provided by the high symbiont concentration. This is presumably the reason for the small activity zone of the study population and the absence of any local movements. However, one would expect differences to occur within a single species - depending on its environment. In areas where seasonal ungulate migrations occur due to a decrease in water supplies and/or poor grazing conditions oxpeckers can only survive by following the symbiont movements. In this respect it may be said that local movements occur in the case of those individuals which survive in greater numbers if they leave, than if they remain in their breeding grounds for the non-breeding season. The distances travelled by these birds are correlated with their requirements and the conditions prevailing at the particular time of the year.

The red-billed oxpecker, in fact, is a bird, which, due to its gregarius instinct and sociality lives harmoniously at relatively high densities. Since home range is fundamentally an area with a certain productivity that meets the energy requirements of the individual or group that occupies it (Jewell 1965), the home ranges of the oxpecker can be correlated with the distribution and concentration of their mammalian symbionts and that the size of the home ranges may vary from one area to another. Seasonal variations may also occur in individual home ranges of the oxpecker since their symbionts are mobile species. In addition, to these possible long-term effects, factors such as sudden climatic changes, variation in the availability of water and food, fires or predation could also effect the size of an individual home range. Moreover, it would appear that the small home ranges observed also suggest a very high symbiont concentration in the Skukuza area.

That individual birds are resighted in particular areas is an indication that the birds are well acquainted with all the features of the terrain within their home range. Here they are familiar with the areas utilised by their mammalian symbionts and could thus find their symbionts with use of minimum energy. Furthermore, the home range habit stabilises the community organization by reducing the amount of turmoil that would result if all the birds were constantly moving about (Dice 1952).

CHAPTER 7

THE MOULT CYCLE

Introduction

Birds periodically shed and renew their plumage by a process known as moulting. Every species exhibits a definite sequence of plumages and moults. In most species there is only one complete moult each year, and its timing is as important to the bird as is the timing of the breeding season (Ledger 1969). Little quantitative information is available on moult in any African bird species. The moulting seasons of most populations are only very imprecisely known, and the duration of moult in individual birds still requires investigation (Siegfried 1971). A review of the literature indicated that no data is available on the moult of the oxpecker. This study was undertaken to obtain an indication of the timing and duration of the moult in the oxpecker, so that moult could be related to other events in their annual cycle.

Results

Moult in adult birds

Primaries

The red-billed oxpecker has ten primaries with the outermost primary much reduced. These primaries were numbered from the carpal joint outwards as suggested by Ledger (1969). Data on the moult of the primaries is summarised in Tables 17 and 18. The primaries of the oxpecker have a sharply defined moulting season, which extends over an 11 month period from September to July (Fig. 17). The onset of primary moult during 1973 was 17 August. This was, however, only one bird from a total of 15 examined. No adult birds were recorded moulting primaries during August 1974 (n = 8). It can therefore be speculated that the onset of primary moult of the oxpecker is early September in the Kruger National Park. Oxpeckers replace their primaries in a very regular sequence, starting with the first and ending with the tenth. A more or less strict symmetry was found between the two wings.

Table 17 : Moult of the primary remiges in 253 adult red-billed oxpeckers in the Skukuza area during the period March 1973 - December 1974.

Month and year	Number individual birds examined	Primary Moult Score			Per cent birds growing primaries									
		Range	Mean	SD	1	2	3	4	5	6	7	8	9	10
1973														
March	18	20-44	34	34,38						8	46	17	21	8
April	9	32-50	42	32,5							11	22	53	33
May	6	42-50	45	20,74									75	25
June	14	44-50	49	6,0									100	
July	11	0	0	0										
August	15	0	0	0										
September	10	1-3	1	3,32	100									
October	13	1-12	6	14,04	20	70	10							
November	16	8-15	10	19,7		14	72	14						
December	11	8-25	16	25,69	10	30	20	40						

Table 17 Continue : Moult of the primary remiges in 253 adult red-billed oxpeckers in the Skukuza area during the period March 1973 - December 1974.

Month and year	Number individual birds examined	Primary Moult Score			Per cent birds growing primaries									
		Range	Mean	SD	1	2	3	4	5	6	7	8	9	10
1974														
January	14	11-30	21	30,89			14	28	42	4				
February	21	12-36	24	47,32			5	17	39	22	11	5		
March	9	21-33	27	23,71					33	33	33			
April	9	28-50	36	15,94						18	27	27	18	9
May	5	43-50	46	15,30									66	33
June	8	43-50	48	18,79									66	33
July	8	41-50	48	7,14										100
August	8	0	0	0										
September	13	1-8	3	10,49	50	50								
October	11	1-8	3	7,62	70	30								
November	7	0-18	8	15,0		50	25	25						
December	17	4-25	15	19,13	10		50	30	10					

Table 18 : The number of growing primaries per wing of 136 adult red-billed oxpeckers in various stages of primary moult in the Skukuza area during the period March 1973 - December 1974.

Primary moult score range	Sample size	Number of growing primaries	
		Range	Mean
1-10	38	1-2	1,0
11-20	27	1-2	1,0
21-30	29	1-2	1,0
31-40	22	1-2	1,2
41-50	20	1-3	1,5

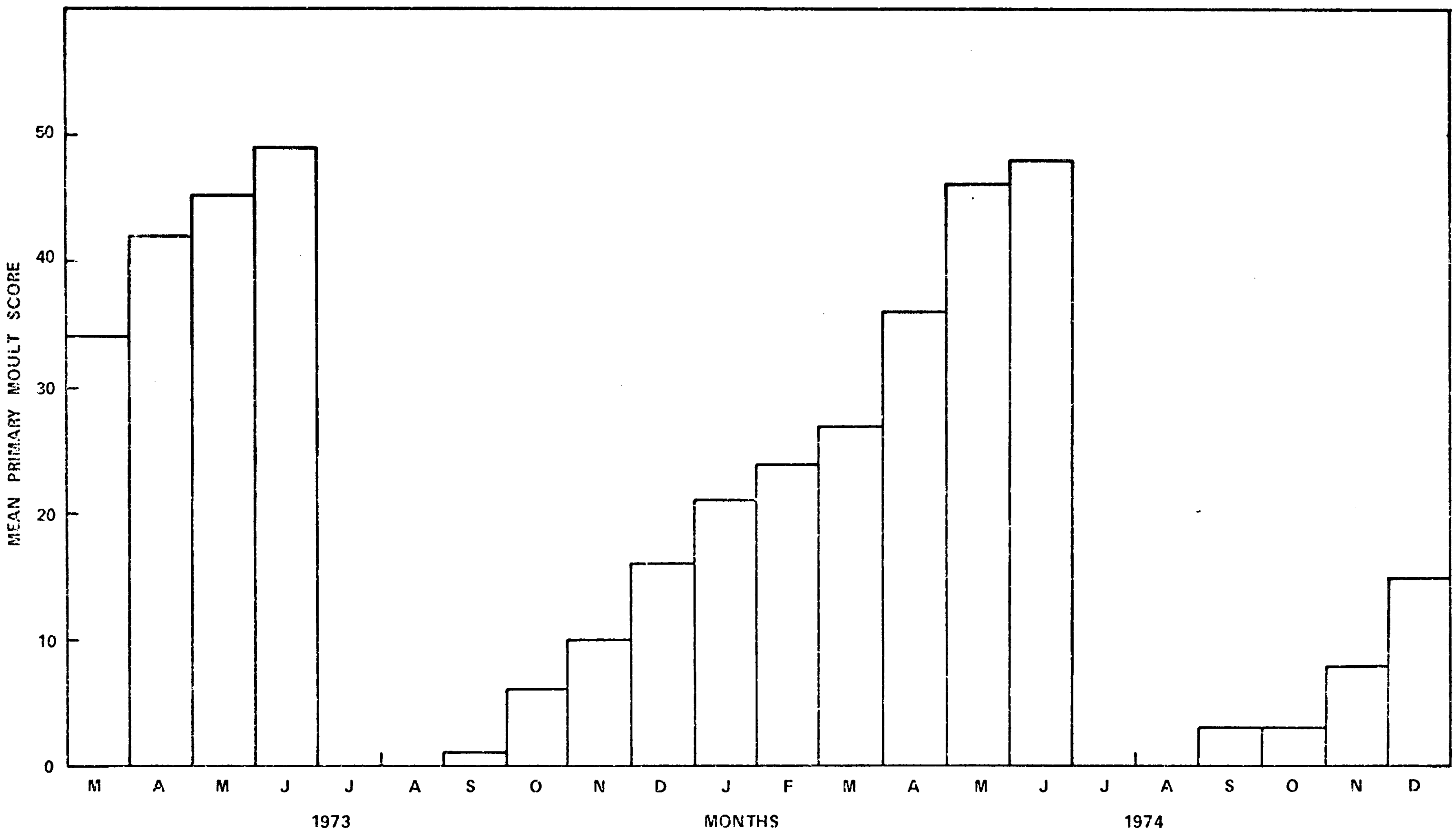


Fig. 17. The mean primary moult score of adult red-billed oxpeckers in the Skukuza area during the period March 1973- December 1974.

The relationship between the time of year and primary moult is given in Fig. 17. These data were analysed statistically and a test on the coefficient of correlation showed that there is a highly significant relationship (t-test, $P < 0{,}05$) between time and the primary moult score with $r = 0{,}98$. Since the samples are heterogenous and are probably not normally distributed around a single mean with respect to date of onset of moult, it has not seemed worth while to calculate a regression line which should give the average rate of progress of primary moult. Instead, mean values have been calculated for successive groups of moult scores. From these results, however, it can be speculated that the primary moult score progresses at a similar rate throughout the moulting period. For individual birds retrapped several times the mean time to replace a primary feather was calculated as 34d ($n = 3$, $SD = 5{,}66$). This gives an average duration of 340d for the complete sequence of primary moult in adult birds. Considerable individual variation occurred. Except at the very end of the primary moult, usually one, less commonly two, adjacent primaries were growing in each wing (Table 18). The reason for this could be that lift is importantly dependent on the length of the leading edge of the wing (Blake 1971). As the last primary is short and relatively unimportant in flight, they are dropped soon after primary nine. The number of primaries growing concurrently in each wing depends both on the intervals between the shedding of the old feathers and the growth rates of the new ones. The long primary moulting period, therefore, seems to be due to the fact that few feathers are grown together and a slow growth rate of individual feathers. Only in one individual were three adjacent primaries found to grow simultaneously. This could have been due to the occurrence of accidental loss of feathers. A considerable variation was apparent in the stage of moult among members of the adult population in any particular month (Table 17). This could be a bias originating from the lack of identification of first-year birds after eight months of age.

Secondaries

According to Ledger (1969) the secondaries are the six outermost remiges attached to the ulna. The secondaries were numbered from the carpal joint inwards. Data on the moult of the secondaries is summarised in Table 19. Table 20 shows the relation of the moult of the secondaries in relation to the primary moult score.

In the red-billed oxpecker a variation occurs in the secondary moult sequence from the typically passeriform moult sequence where the secondaries moult centrifugally. In the oxpecker the moult of the secondaries is initiated at two points (moult centers), at the first secondary and at the innermost secondary. The first secondary is shed at a primary moult score of about 21 during January and the innermost secondary at a secondary moult score of about 26 during April. The two waves of moulting feathers then converge and meet at about the 4th secondary. The earliest record of an adult bird moulting secondaries is on 23 December 1973. This was, however, only two birds from a total of 11 examined. No adult birds (n = 17) were recorded moulting primaries during December 1974. The secondary moult cycle, therefore, extends over a seven month period, January to July. The primary and secondary moult ends at about the same time in July. Considerable individual variation occurred in the stage of secondary moult (Table 19). Although there is a strong tendency to symmetry in the moult of the secondaries, the score for the two wings were not often identical. There were also more irregularities seen in the moult of the secondaries than in the moult of the primaries.

Tertials

The three remiges in the oxpecker were numbered from the distal to the proximal side of the wing. The tertials moult in the normal middle/inner/outer passeriform fashion. Both the middle and innermost tertials are well developed before the outermost tertial breaks from the sheaths. Data on the

Table 19 : Moult of the secondary remiges in 250 adult red-billed oxpeckers in the Skukuza area during the period March 1973 - December 1974.

Month and year	Number individual birds examined	Secondary Moult Score			Per cent birds growing secondaries									
		Range	Mean	SD	1	2	3	4	5	6	7	8	9	10
1973 March	17	0-27	10	26,65	13	40	26	13		6				
April	9	6-30	14	24,64	50	16	33							
May	5	11-18	14	13,93		60	40							
June	12	13-30	25	26,96			50	50						
July	11	28-30	29	20,42										
August	16	0	0	0										
September	10	0	0	0										
October	13	0	0	0										
November	16	0	0	0										
December	11	0-1	0	0	100									

Table 19 Continue : Moult of the secondary remiges in 250 adult red-billed oxpeckers in the Skukuza area during the period March 1973 - December 1974.

Month and year	Number individual birds examined	Secondary Moult Score			Per cent birds growing secondaries									
		Range	Mean	SD	1	2	3	4	5	6	7	8	9	10
1974														
January	14	0-5	1	5,39	100									
February	20	1-10	2	12,21	60	40								
March	9	1-5	2	6,08	80	20								
April	10	0-19	11	24,19	22	11	22	22	22					
May	5	11-30	20	16,67			20	20	40	20				
June	8	22-30	28	7,48				60	20	20				
July	9	7-30	25	21,26			50			50				
August	8	0	0	0										
September	13	0	0	0										
October	11	0	0	0										
November	7	0	0	0										
December	17	0	0	0										

Table 20 : Remex moult score of 250 adult red-billed oxpeckers in the Skukuza area in the period March 1973 - December 1974.

Month -	1973										1974											
Moult Score	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Primaries (50)	34	42	45	49	0	0	1	6	10	16	21	24	27	36	46	48	48	0	3	3	8	15
Secondaries (30)	10	14	14	25	29	0	0	0	0	0	2	2	11	20	28	25	0	0	0	0	0	0
Tertials (15)	4	11	0	0	0	0	4	8	0	0	1	7	10	12	0	0	0	0	6	11	13	0

moult of the tertials is summarised in Tables 20 and 21. The oxpeckers has two clearly defined tertial moult cycles in a year, each lasting between three and four months. The first begins at the same time as the primary moult cycle in September and lasts until November. The second begins in January at the same time as the secondary moult cycle and lasts until April. A considerable variation in the stage of moult of the tertials was found in individual birds. As in the case of the secondaries the tertial moult score was often not identical in the two wings although the same moulting trend was followed.

Primary coverts

Moult of the primary coverts is summarised in Table 22. The ten primary coverts are lost one at a time along with the corresponding primaries. The primary covert moulting season thus also extends over a 11 month period from September to July.

Secondary coverts

Data on the moult of the secondary coverts are summarised in Table 22. The six secondary coverts are lost one at a time. The progression of moult in this series is from the outermost inwards. From Table 22 it appears that the oxpecker has two secondary coverts moult cycles annually - one before and one after the breeding season which corresponds with body moult. The first secondary moulting session starts at about the same time as the moult of the primary coverts (i.e.) that is before the moult of their corresponding secondaries. It can thus be concluded that in the oxpecker there are no relationship between the secondary coverts moult cycle and the secondaries moult cycle and that the secondary coverts moult independently of the secondaries.

Lesser coverts, median coverts, axillaries and underwing coverts

Data on the moult of these regions is summarised in Table 22. It appears that these regions have two moult cycles annually which resemble the body moult cycles and the moult

Table 21 : Moult of the tertial remiges of 264 adult red-billed oxpeckers in the Skukuza area during the period March 1973 - December 1974.

Month and year	Number individual birds examined	Tertial moult score			Percent birds growing tertials		
		Range	Mean	SD	1	2	3
1973							
March	18	0-12	4	14,14	40	40	20
April	9	1-15	11	5,66	33		66
May	6	0	0				
June	14	0	0				
July	11	0	0				
August	15	0-1	0	1,41		100	
September	10	2-7	4	4,69	10	60	30
October	13	3-15	8	15,39	14	28	56
November	16	0	0	0			
December	15	0	0	0			
1974							
January	13	0-5	1	6,56	16	84	
February	22	1-15	7	30,94	8	58	33
March	13	1-15	10	18,71	12	64	24
April	10	7-15	12	15,78	40	20	40
May	5	0	0	0	100		
June	7	0	0	0			
July	9	0	0	0			
August	8	0	0	0			
September	17	1-8	6	5,66	28	24	48
October	10	2-15	11	15,68	44	28	28
November	7	6-15	13	11,05	50		50
December	16	0	0	0			

Table 22 : Progression of moult in different feather regions, expressed as the percentage of birds showing moult for 253 adult red-billed oxpeckers in the Skukuza area in the period March 1973 - December 1974.

Month -	1973										1974											
Feather region	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Forehead	100	100	100	100	81	100	100	100	93	100	93	100	100	100	100	100	100	100	100	100	100	88
Crown	100	100	100	31	54	81	100	100	44	82	78	100	100	100	100	88	33	100	100	100	100	52
Chin	100	100	100	92	72	100	100	100	93	72	93	95	100	100	100	88	100	100	100	100	100	100
Cheek	100	89	85	92	81	100	100	100	93	90	93	95	100	100	100	88	100	100	100	100	100	100
Nape	96	100	71	15	0	56	100	100	6	81	71	95	100	100	40	11	11	57	100	100	100	41
Neck	96	78	71	15	0	50	100	100	6	81	71	95	100	100	40	18	22	57	100	100	100	41
Mantle	96	89	57	0	0	31	100	100	6	72	64	91	100	100	0	11	0	42	100	100	83	17
Back	96	89	57	0	0	12	100	100	19	54	64	95	100	100	0	0	0	42	76	100	83	11
Rump	96	89	28	0	0	12	100	100	25	36	50	83	100	100	0	0	11	14	92	100	83	0
Upper tail coverts	100	22	28	15	0	12	80	76	25	36	43	73	100	83	0	0	11	14	76	100	100	35
Breast	100	67	14	0	0	12	100	100	12	36	64	91	100	100	0	0	0	42	100	100	83	6
Abdomen	96	78	14	0	0	6	100	100	6	27	50	83	100	100	0	0	0	14	100	100	83	0
Flank	96	100	14	0	0	0	100	100	6	63	57	91	100	100	0	0	0	14	100	100	83	0
Undertail coverts	96	44	14	0	0	0	70	69	25	36	36	63	100	83	0	0	11	14	76	100	100	23
Lesser coverts	96	55	28	0	0	6	80	100	0	18	21	54	87	83	0	0	11	0	100	85	33	0
Median coverts	96	55	14	0	0	6	90	92	0	45	21	36	100	83	0	0	11	0	100	71	16	0
Secondary coverts	100	77	42	0	0	6	100	100	19	63	57	73	100	100	0	33	33	0	46	57	16	6
Primary coverts	100	66	28	0	0	6	100	76	100	100	93	95	100	83	40	18	22	0	76	71	66	100
Bastard wing	50	11	0	0	0	0	0	0	0	0	0	18	62	66	0	0	0	0	0	0	0	6
Axillaries	100	77	42	0	0	19	100	100	12	72	57	86	100	100	0	0	33	57	100	85	83	6
Underwing coverts	96	77	28	0	0	6	70	100	6	9	50	73	100	100	0	0	11	0	100	71	16	0
Tail	100	66	42	15	0	13	60	92	37	58	57	76	100	100	40	25	0	28	30	60	71	47

of the tertials. The first cycle corresponds with the beginning of the primary moult and the second cycle with the start of secondary moult or with a primary moult score of about 21. However, from Table 22 it is clear that a tremendous overlap occurs between the two cycles which could be due to individual variation. The first underwing series to be moulted is the marginal coverts on the underside of the forearm.

Bastard wing

From Table 22 it is clear that the three main feathers of the alula moult only once annually. Their moult cycle corresponds with the start of the secondary moult and the complete body moult cycle after the breeding season in February. The main alula feathers are lost one at a time starting with the most proximal feather. Moult commences from February to April or between a primary moult score of 24 and 36.

Rectrix moult

The 12 rectrices of the oxpecker were numbered in pairs from the central pair outwards. Data on the moult of the rectrices is summarised in Tables 23 and 24. Moult of the rectrices occurs in the order 6-1-2 or 5-3-4. These results were obtained from birds frequently retrapped. Rectrix moult was usually highly assymetrical and a high occurrance of accidental loss of feathers frequently masked the basic pattern which was in progress. In the oxpecker the rectrices moulted only once annually from August to June. From Fig. 18 it appears that the tail feathers started to moult before the primaries in August but the moult was completed at the same time as the primary moult in July. As only 13% of the birds were moulting tail feathers during August 1973, it could be speculated that the main trend of retrix moult corresponds with that of the primary moult cycle and that the differences were due to individual variation or accidental loss of feathers. However, 28% of the birds were moulting tail feathers in August 1974 with the first primary moult observed in September. From these results it could be

Table 23 : Per cent growing rectrices in adult red-billed oxpeckers in the Skukuza area during the period March 1973 - December 1974.

Month and year	Left side						Right side					
	1	2	3	4	5	6	6	5	4	3	2	1
1973												
March	17	7	4	6	6	4	9	10	7	3	7	17
April		15	31	15		7	7		15	7		
May			25	37					12	12	12	
June				100								
July												
August	50				50							
September	16	16	16		8			16		8	8	8
October	14	14		7	7	10	17			3	14	14
November	28		18			38		8		8		
December	5	17	5	5	11	11	5			17	5	11
1974												
January		6	12	6	12	6		12		6	11	6
February	20	3	6		13	6	10	16	3	3	6	10
March	10	13	8	2	10	2	5	16	5	2	10	10
April	9	13		9	13	13			9	4	13	13
May				25		25			25			25
June	33			33							33	
July												
August							50					50
September	11	5		5	16	16	27	5		5	5	
October	11			11		11	44					22
November						50	16				16	16
December	14						86					

Table 24 : Number of rectrices moulting in one tail of 123 adult red-billed oxpeckers in the Skukuza area in the period March 1973 - December 1974.

Number of feathers	Number of cases	Percentages of total
1	48	39
2	26	21
3	24	19
4	14	11
5	9	7
6	2	1

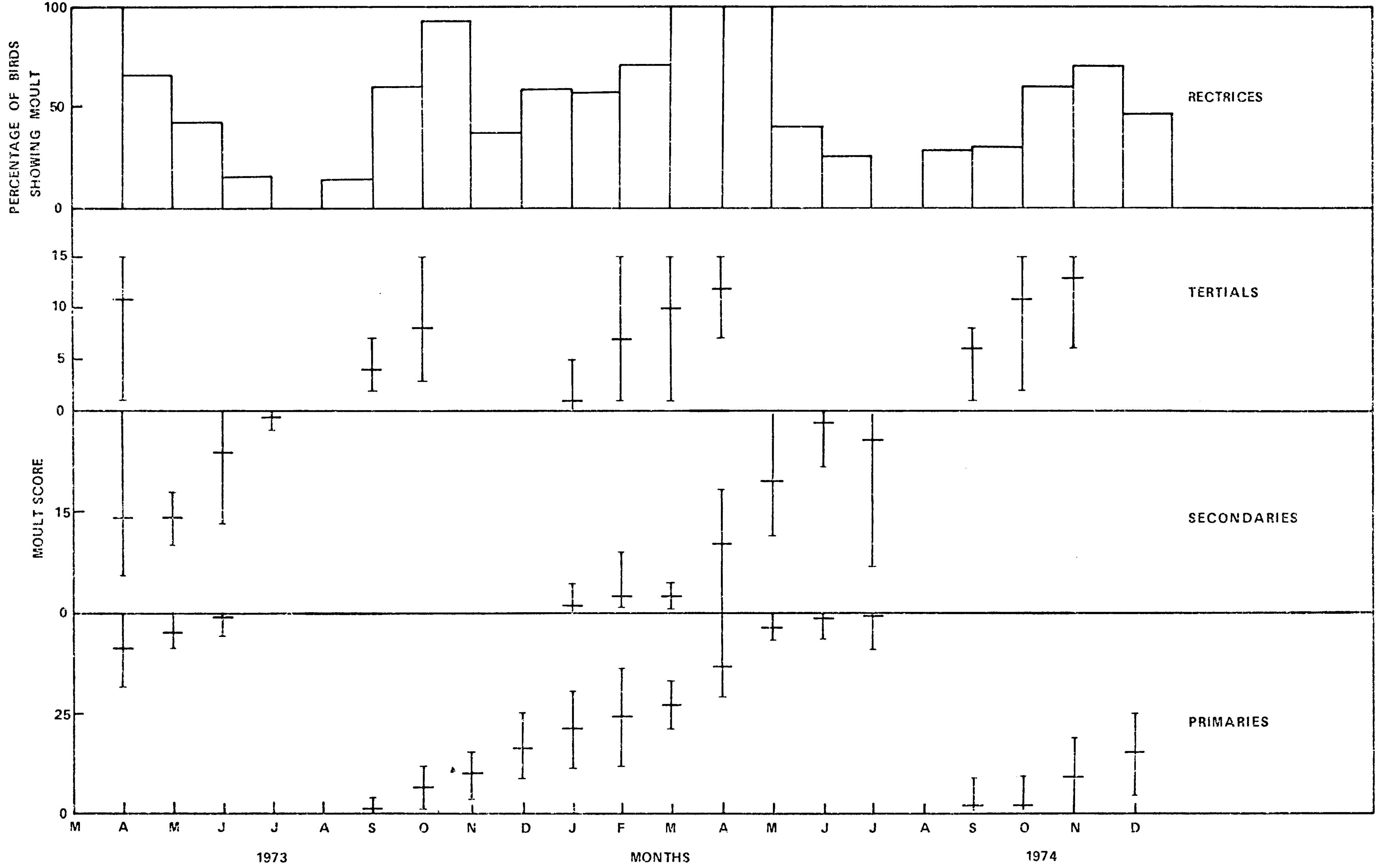


Fig. 18. Moult of the adult red-billed oxpecker in the Skukuza area during March 1973- December 1974. Vertical lines is the range with horisontal lines the mean.

postulated that in the oxpecker rectrix moult starts before primary moult in the Kruger National Park.

In Table 24 information is given on the actual number of feathers recorded moulting in any one tail of adult birds. The figures show that in the majority of cases only one feather was moulting (39%) at a time. However, cases where two to four feathers were moulting at the same time, although perhaps in different stages of moult, were fairly common (14 - 26%). In relatively few cases five or six feathers were moulting at the same time (9% and 2% respectively). Only two cases where more than six feathers were moulting, were recorded.

Moult of the body areas

Data on the moult of the body areas is summarised in Table 22. Two complete body moult cycles can be distinguished, September to October and March to April. However, due to considerable individual variation, body moult was found to occur throughout the whole moult period, from August to April. The basic sequence for body moult is head-neck-back-rump and head-neck-breast-abdomen. These two body moult cycles correspond with the moult of the tertials. From Table 23 it appears that in a few head regions (forehead, chin and cheek) moult is constant throughout the year and is not restricted during the winter months. This could be due to feather wear that involves replacement of feathers. There appears to be no relationship between the moult of the upper and undertail coverts and the moult of the rectrices, with the rectrices having only one moult cycle per year (Table 22). During 1973 the uppertail coverts started to moult before the undertail coverts. In 1974, however, no difference was found in the onset of moult of these series.

Moult pattern in first-year birds

Only moult of birds after leaving the nest is considered in this chapter. The red-billed oxpecker breeds during the summer months from October to March, with three breeding sessions. Three age classes can thus be distinguished in first-year birds. The moult pattern in first-year birds is further complicated by the inability to distinguish first-year birds from adult birds after about eight months. However, by using first-year birds retrapped several times and by using the percentage moult observed in each month, the main trend of postjuvenal feather replacement can be followed.

Data on the moult of the first-year birds is summarised in Table 25. It appears that the birds undergo a partial postjuvenal feather replacement at about three months of age. In this cycle all the feathers are replaced except the primaries, secondaries, rectrices and the primary coverts. From Table 25 it appears that the rectrices are replaced during this cycle but data obtained from retrapped birds shows that this is only an accidental loss of feathers and not a complete moult cycle. The rectrices are also not fully grown when the young birds leave the nest, which explains the 100% rectrices moult obtained from December 1973. This partial postjuvenal feather replacement is completed during May (Table 25).

In September or October, the juveniles began to moult again. From retrapped birds it was apparent that this is a complete moult cycle which corresponds with the complete moult cycle of the adult birds at the beginning of the rainy season (Tables 20 and 22). From Table 25 and from data obtained from retrapped birds it is clear that the postjuvenal feather replacement follows the same pattern as adult moult. For individual birds the length of the postjuvenal feather replacement is not known. The moulting season of juveniles, however, is restricted to a particular period of the year.

Timing of moult

In summary, the oxpecker starts moulting with the beginning of the rainy season in August. Body moult is completed or delayed with the onset of the breeding season in late October but a moult-breeding overlap occurred in the rectrices, primaries and primary coverts. A post-nuptial body

Table 25 : Progression of moult in different feather regions, expressed as the percentage of birds showing moult, for 95 first-year red-billed oxpeckers in the Skukuza area in the period December 1973 - October 1974.

Month - Feather region	1973	1974									
	Dec	Jan	Febr	March	April	May	June	July	Aug	Sept	Oct
Primaries	0	0	0	0	0	0	0	0	0	0	100
Secondaries	0	0	0	0	0	0	0	0	0	0	0
Tertials	0	0	0	28	57	33	0	0	0	100	100
Tail	100	0	14	57	28	0	0	0	0	33	100
Forehead	0	25	66	71	71	100	100	0	100	100	100
Crown	0	0	50	57	71	66	40	0	100	100	100
Chin	0	25	66	85	71	100	100	0	100	100	100
Cheek	0	25	66	85	71	100	100	0	100	100	100
Nape	0	0	33	57	71	33	20	0	100	100	100
Neck	0	0	33	57	71	33	20	0	100	100	100
Mantle	0	50	50	85	71	22	0	0	75	100	100
Back	0	25	60	85	71	22	0	0	25	100	100
Rump	0	25	33	71	71	22	0	0	0	88	100
Uppertail coverts	0	0	33	71	57	22	0	0	0	66	100
Breast	0	25	66	71	71	22	0	0	25	100	100
Abdomen	0	25	66	71	71	22	0	0	0	88	100
Flank	0	50	66	85	71	11	0	0	0	88	100
Undertail coverts	0	50	33	57	57	22	0	0	0	88	100

Table 25 Continue : Progression of moult in different feather regions, expressed as the percentage of birds showing moult, for 95 first-year red-billed oxpeckers in the Skukuza area in the period December 1973 - October 1974.

Month - Feather region	1973 Dec	1974 Jan	Febr	March	April	May	June	July	Aug.	Sept	Oct
Lesser coverts	0	0	33	85	71	33	0	0	0	66	100
Median coverts	0	0	16	57	57	55	0	0	0	55	100
Secondary coverts	0	0	0	14	57	33	0	0	0	88	100
Primary coverts	0	0	0	0	0	0	0	0	0	0	100
Bastard wing	0	25	50	85	71	22	0	0	0	44	0
Axillaries	0	0	0	14	14	11	0	0	0	0	100
Underwing coverts	0	0	50	85	85	44	0	0	0	100	100

moult started after or near the end of the breeding season during February which is completed at the end of March at about the same time as the end of primary, primary coverts and rectrix moult. Figure 18 shows the relationship between the mean primary, secondary, tertial moult scores and the percentage birds moulting rectrices. There appears to be a difference in the onset of moult in the oxpecker in the 1973 and 1974 moulting seasons with an earlier start during the 1973 moulting season. This could be related to the differences in the onset of breeding found in the onset of breeding in the 1973/74 and 1974/75 breeding seasons (Stutterheim in prep.). The data are in general insufficient as yet to determine differences in the timing of moult in years due to age or sex.

Discussion

The timing and sequence of the moult are closely adapted to the ecological circumstances of each species (Snow 1969). Even within the same species, geographical differences and migratory behaviour may be associated with different moult regimes. In the oxpecker, the feathers of the primaries and tertials are moulted in the sequence typical for passerines - the primaries from the innermost outwards and in the tertials the central one is shed first, followed by the inner and then the outer. The typical passerine moulting sequence for the secondaries are from the outermost inwards and for the rectrices from the central pair outwards (Newton 1968). In the oxpeckers, however, the moult of the secondaries is initiated at two moulting centers, the innermost and outermost secondary, and these two waves of moulting feathers then meet at about the 4th secondary. Moreover, the moult of the rectrices in the oxpecker occurs in the order 6-1-2 or 5-3-4.

A review of the recent literature (Newton 1968; Flegg and Cox 1969; Murton _et al_. 1969; Snow 1969; Baggott 1970; Bell 1970; Pearson 1973; Holyoak 1974; Green and Summers 1975 and Pearson 1975) indicates that the mean estimated moult duration of passerine birds as obtained from regression analysis, was calculated as 75d (n = 31, SD = 46). This can be compared to the exceptional long duration of primary moult of 340d in the oxpecker. Moreover, in the oxpecker, the mean number of primaries that was growing together was calculated as 1,14 (SD = 0,7) and the mean time to replace a primary feather 34d (SD = 5,66). In a review of the moult regime by Pearson (1973), in a total of 8 passerine species with a mean duration of primary moult of 57d the mean number of primaries that were growing together, was calculated as 3,13. The long primary moulting period in the oxpecker, therefore, seems to be due to the fact that few feathers are grown together and a slow growth rate of individual feathers.

Since the plumage comprises approximately ten per cent of the total mass of a bird, replacement of the plumage requires a considerable expenditure of energy (Humphrey and Parks 1959). Moult is a period of intense metabolic activity and in many British bird species, moult is a period of relative inactivity (Bell 1970). In many species the breeding is so timed that the birds are raising young when food is most abundant (Lack 1954). The adults must therefore delay their moult if they are to be most efficient when finding food for their young. The oxpecker, however, delays only the moult of the body areas, secondaries and tertials during the breeding season while the primaries and rectrices continue moulting. To devote excess energy and nutrients of the reproducture period to nonreproductive activities such as moult is not disadvantageous as long as these activities in no way interfere with reproduction (Foster 1975). Certainly, incomplete moults consume less energy than complete moults in terms of replacement costs. Newton (1966) found that in the bullfinch (Pyrrhula pyrrhula), a temperate species, body feathers comprise 69,1% of the total feather weight, whereas remiges and rectrices and their associated coverts comprise only 22,4% and 8,5%, respectively.

In the swallow-tailed gull (Creagrus furcatus), experimental removal of two adjacent primaries (3rd and 4th, or 5th and 6th) from each wing of both birds in a pair does not impair the ability of pairs to raise young (Harris 1971). In the oxpecker, it can thus be speculated that moulting of the primaries and rectrices in the breeding season does not hamper breeding in adult birds.

Payne (1969) reviewed the literature on the overlap of breeding and moulting schedules in African birds. He found that only 3,8% of the birds he examined (190 species), showed an overlap and that most instances of overlap occurred either near the beginning or at the end of the breeding season. Moreover, overlap seems to be more prevalent among certain families and genera. In the oxpecker, moult occupies a substantial part of the annual cycle of individual birds and the moult period of the study population overlapped with the breeding season and was as a whole longer than the breeding season. Presumably food is limiting in birds and temporal spacing has evolved in response to high requirements of each event (moult and reproduction are two of these resource-demanding events). Thus an activity is timed to occur when environmental conditions are favourable and when interference from other activities is minimal. Foster (1975) speculates that if a species utilises food sources that are extremely abundant for a very short period, and so limited at other times, then both moult and breeding must be completed during this period of super abundance. If this period is short enough, the two activities must occur simultaneously. Foster (1975) also speculates that one may explain overlap of moult and breeding in some species through a reduction in energy required for moult and/or breeding so that enough is available for both activities to occur simultaneously. Reproductive cost may be reduced in a variety of ways. The oxpeckers occupy natural cavities that they use without modification for nesting and are co-operative breeders (see section under breeding behaviour). Rowley (1965), however, found that the superb blue wren (Malurus cyaneus) (which is a co-operative breeder) only moulted after the breeding season and about six weeks after laying the last egg. Furthermore, since pairs nested at different times the onset of the moult was not uniform within the population. In the oxpecker, the energy requirement for moulting could also be reduced by a long moulting season and delaying body moult during breeding. Breeding is triggered in the oxpecker by the onset of the rains or by some other environmental factors whose date of initiation may vary from year to year (Stutterheim in prep.). Thus, if the postnuptial - moult period is fixed to a particular part of the calendar, the ability to overlap moulting and breeding may be significant in allowing renesting in those years when the environmental trigger for breeding is "late" (1974/75 breeding season). It would also allow individuals to begin breeding as soon as favourable conditions arose, even in years when the environmental trigger was "early" and the birds were still in prenuptial moult.

CHAPTER 8

BREEDING BIOLOGY

Introduction

Up to date there have been few original descriptions of the breeding behaviour of the red-billed oxpecker (Jackson 1938; Benson 1946 and Van Someren 1951, 1956), and these only describe the breeding behaviour of the oxpeckers in broad terms.

Study area

The present study was carried out in the Satara and Nwanedzi areas of the Kruger National Park (Fig. 1). This area was chosen because of high ungulate concentrations, and concomitant high concentration of oxpeckers (Stutterheim in prep.).

Climate

Two seasons characterise the climate of the area. The cool dry season, from May to August, which warms up in September and October, to the hot wet season (subject to periodical rainfall restrictions) from October to April (Kemp 1972).

Geology

The area, with a slight eastern aspect, is divided by a north-south line of sandstone outcrops in the western third of the park, and bounded on the eastern side by the low hills of the Lebombo range. The area is intricately furrowed by the drainage lines of many seasonal rivers and streams, a few draining to the Timbavati river on the north and west corner of the study area, but mostly draining to the east to pass through the Lebombo hills of the Nwanedzi gorge.

The sandstone divide also separates the geology into Ecca sandstone on the west and Stormberg sandstone of the

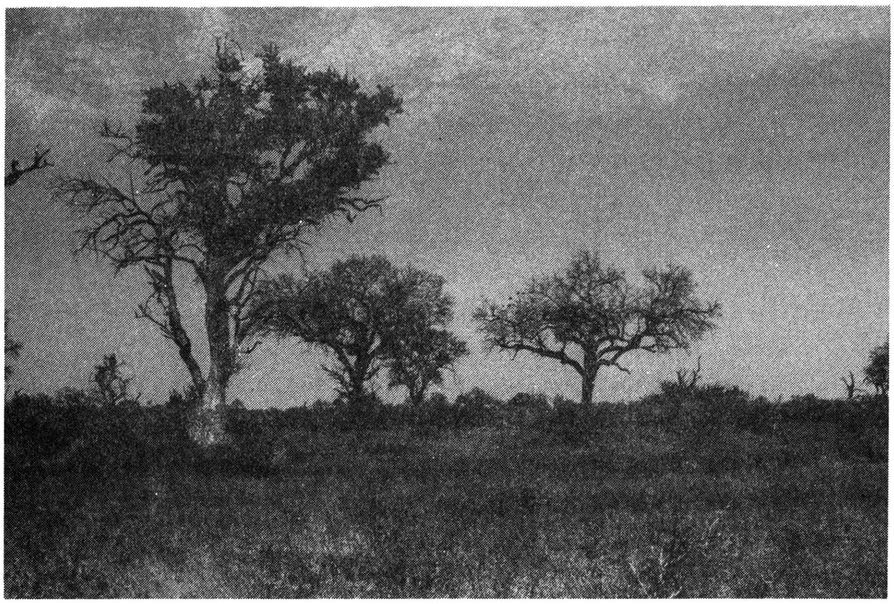
Karroo series on the east. The soils to the east, also of the Karroo series, are basaltic, dark and heavy. The granitic soils to the west are pale and sandy. On the extreme east, the basalt soils grade into the rhyolite of the Lebombo hills (Kemp 1972).

Vegetation

The vegetation is dependent on the soil types, and four main vegetation associations are found in the study area. On the basalt soils to the east, *Acacia nigrescens* - *Sclerocarya birrea* parkland savanna predominates with scattered trees about 15 m high, a stratum of low scattered bushes, and a dense grass cover (Plate 10). *Acacia nigrescens* is dominant over *Solerocarya birrea* in the association. Other tree species commonly found in the area being *Launea kirkii*, *Acacia tortilis*, *Combretum imberbe*, *Lonchocarpus capassa*, *Diospyros mesptiliformes* and *Albizzia harveyi*. The main species in the bush stratum are various *Grewia* species, *Dahlbergia melanoxylon*, *Dicrostachys cinereus* and *Commiphora* species, with *Euclea divinorum*, *Acacia exuvialis* and *Terminalia prunniodes* predominating to the north and east of the study area. In these latter regions the parkland gives way to a denser bushy association, dominated by bushes and small trees of *Acacia nigrescens*. The dominant grass cover in the area is *Bothriochloa insculpata*. Along the extreme eastern edge of the area where the Lebombo rhyolite appears, *Combretum apiculatum*, *Acacia tortilus* and *Euphorbia* species become most evident.

To the west of the sandstone reef, the vegetation is mixed *Combretum* savanna. In the study area, large *Acacia nigrescens* trees still create a parkland conformation, but there is a predominance of *Combretum* species, especially *Combretum apiculatum*, and in some areas these form dense bush associations. Other trees that are most common in the western half of the area are *Bolusanthus speciosus*, *Sclerocarya birrea*, *Terminalia sericea*, *Terminalia prunnoides* and *Acacia gerradi*. The grass cover of several species has a density inversely proportional to the density of the bush

Plate 10. *Acacia nigrescens* - *Sclerocarya birrea* parkland savanna in the Satara area, October, 1974.



cover, but the main cover is still of Bothriochloa insculpata in the open areas.

A dense parkland association occurs along the sandstone divide and the banks of the watercourses for some distance further east. The dominant trees are Acacia delagoensis, Spirostachys africanus, Diospyros mesptiliformes and Combretum imberbe. The bush stratum is also dense, mainly Euclea divinorum and Dicrostachys cinereus, but grass cover is sparse.

A fourth vegetation type is found along the water-courses, where there is much underground water and many trees are evergreen and over 25 m high. Acacia xanthophoea occurs on the most poorly drained soils, and the commonest trees are Acacia robusta, Diospyros mesptiliformes, Ficus sycomorus, Kigelia pinnata, Pseudocadia zambesiaca and Schotia brachypeltata. The bush stratum is often dense, mainly of Euclea, Crewia, Salix and Maytenus species. The mixed grass cover is high and often dense (Kemp 1972).

Results and discussion

Behaviour patterns associated with breeding

Copulation

Pitman (1956) reported that the nuptial display and the act of coitus in the red-billed oxpecker takes place on the backs of the mammalian symbionts but gives no further information. Copulation was only observed four times - three times on the backs of the symbionts and once on the ground in the absence of any mammalian symbionts. Copulation was not observed at or near the nest. The nuptial display consists of the two birds lowering their bodies, opening their bills while spreading out the tail and wings horizontally. The two birds then move slowly around each other in circles with rapid vibrating wings. When the male is in front of the female, the female would close her wings, move underneath the males wings, crouch down and lift her tail. Copulation then takes place. Vocalisation during the nuptial display is the contact call. Discriptions of the vocalisation of the red-billed oxpecker are given elsewhere (Stutterheim in prep.).

Courtship feeding

Courtship feeding was observed only once on the back of a giraffe. In the oxpecker, courtship feeding consists of a simple transfer of food from one adult bird to another. The one adult bird was observed to move closer to the other bird, to open its bill and to present the food to the other bird. No begging posture was observed. After the courtship feeding the two birds started feeding again. The relationship between courtship feeding and copulation in the oxpecker is not known.

Wing-flapping display

The wing-flapping display was only observed at the nest during the breeding season. In the wing-flapping display the bird would spread his tail and bend forward while vibrating his wings (Plate 11). This display could be repeated several times. The wing-flapping display was observed in different situations and cannot be described as a greeting or a nest-relief ceremony e.g.:

a. During the nest-searching period when a large enough hole was found, one bird would attract another by giving the display in front of the hole.

b. During the incubation period when an adult bird arrived at the nest, he would give the display when the incubating bird was coming out of the nest.

c. During the nestling period when two birds arrived at the same time at the nest, either both birds or one would display.

d. The wing-flapping display was also given when a predator or a vehicle approached the nest. In this situation the wing-flapping display could be a displacement activity.

Plate 11. The wing-flapping display of the red-billed oxpecker at a nest in the Satara area, December 1974.

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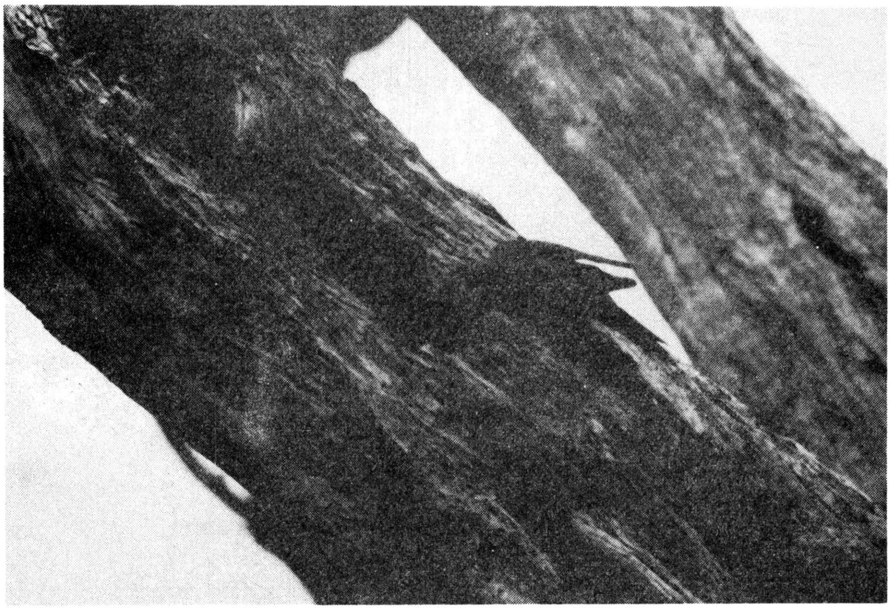

Open-wing display

The open-wing display was only observed at the nest during the breeding season. In this display the bird would bend forward while spreading out the wings. The open-wing display was frequently observed after nest-relief during incubation or after feeding the nestlings. This display can be described as an intention movement in a conflict situation between leaving and staying at the nest. The open-wing display was also observed when a predator approached the nest.

The nest

Selection of the nesting site

Searching for suitable nest holes is always done from the mammalian symbionts. The procedure is that one bird would give the contact call and fly to a suitable nesting tree. This bird was followed by the rest of the group. All the birds in the group took part in the search. However, two birds (the active male en female), searched together and appeared to be more active than the other birds in the group.

One of two such birds was observed to give the wing-flapping display every time a large enough hole was found and would stay at the hole until the other bird entered the hole. These observations were obtained by collecting the birds after every observation. According to Von Haartman (1957) this demonstration at the nesting hole forms part of the courtship display which is an adaptation that occurs in hole-nesting birds. Furthermore, this nest-demonstration has probably developed phylogenetically from displacement nest-building, released in the male by the female.

In a total of eight observations, 75% of the trees searched were leadwood (*Combretum imberbe*), 12% marula (*Sclerocarya caffra*) and 12% knob-thorn (*Acacia nigrescens*). The survival value in searching for a suitable nesting hole from their mammalian symbionts could be to ensure that the breeding site is located in an area utilised by their symbionts. This could also affect nesting dispersion in the sense that more nests would occur in areas frequented by their mammalian symbionts. According to Lack (1968) the type of nesting dispersion involved is advantageous as regards both the safety of the nest and feeding habits. The link between nesting dispersion and diet depends partly on the dispersion for feeding, since many of the birds which feed in flocks, nest in colonies, while the birds which hunt solitarily, nest solitarily. An advantage of solitary nesting as far as feeding is concerned, is that it enables a bird to collect the food for its young near the nest without disturbance from other pairs or groups. Solitary breeding also reduces the conspicuousness of the nest to predators. However, the oxpecker is a solitary nester but was observed to feed in flocks during the breeding season. In addition the oxpecker is also feeding on mobile mammals which are constantly moving around. It would therefore be detrimental for the oxpecker to be a solitary feeder because the distribution of the mammalian symbionts and thus the distribution of the food, could on one day be concentrated in a certain area.

According to Zahavi (pers. comm.)* food must be a limiting factor in the ecology of the oxpecker or at least during certain times. This can be seen by the agonistic behaviour between different groups on the mammalian symbionts e.g.:

a. When one group of birds arrived at a group of mammals where another group was already present, all the birds would gather on one symbiont and adapt the penguin attitude while giving the contact call and the low intensity "alarm" call (Van Someren 1951). This behaviour was possibly to determine the dominance of the group and if food was a limiting factor, one group would displace the other as observed at the onset of the breeding season.

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b. Agonistic behaviour between two individual birds was also observed on the mammals. Here, one bird would displace another for a preferred feeding area. In this display, which appears to be a threat display, one bird would open its bill and move towards another bird which would usually move away. Actual fighting was not observed.

c. During the breeding season it was frequently observed that out of a group of birds one bird would chase another away from a mammal for up to two hundred meters before returning to the mammal. However, as these observations were not done on marked birds, the role and status of individual birds are unknown. From these observations it could be speculated that food may be a limiting factor, or at least during certain times, and could thus also play a role in the dispersion of the birds and the nests.

Nest habitat

The habitat within an approximate radius of 100 m from each nest was divided into two sets of variables as suggested by Kemp (1972) e.g. the vegetation form surrounding the nest site and the distance from the nearest surface water. A total of 87% of the nests occurred in open Acacia nigrescens - Sclerocarya birrea parkland (the dominant vegetation form in the study area), while only 13% of the nests occurred in dense mixed woodland. A significant difference (t-test, $P < 0,05$) was found between the occurrence of nests in these two vegetation forms with more nests in open parkland than in dense mixed woodland. It is noteworthy that a possible bias could be that it is easier to spot a nest in open parkland than in dense woodland. A large percentage of nests (46%) occurred within a radius of 100 m from a watercourse. However, a high percentage of nests along the watercourses could be due to a bias in the distribution of roads.

Nest site

A survey of the literature (Van Someren 1951, Henderson 1953 and du Preez 1971), East African breeding records (Mundy in litt.) and the nest record cards filed at the

Percy FitzPatrick Institute of African Ornithology, gives the following data for nests of the red-billed oxpecker:

height - ground level to 30 m; 28 nests in holes in trees, one nest on ground underneath a boulder, five nests in cracks in stone embarkment and one nest in a nest box. All 43 nests found in the Satara area were natural holes in trees (Plates 12, 13 and 14). The preferred tree species were the following:

Combretum imberbe	84%
Acacia nigrescens	9%
Spirotachys africanus	3%
Colophospernum mopane	3%
Kigelia pinnata	3%

To check whether the observed preferred tree species were not merely a reflection of the dominance of those trees in the area, all trees large enough (higher than 2 m and with a main trunk with a circumference of at least 50 cm) to contain an oxpecker nest and the occurrence of suitable nesting holes were counted in a 16 ha area in the Satara experimental plots. The results of the count is given in Table 26. In this area, two nests were found - both in C. imberbe trees. From Table 26 it is clear that A. nigrescens and S. africanus are the dominant tree species. It is thus apparent that oxpeckers prefer to breed in C. imberbe trees in the Satara area and that this is not representative of the incidence of the tree species in the study area. In the 16 ha area in the Satara experimental plots, however, nesting holes were found in 80% of the C. imberbe trees examined while nesting holes were found in only 14% of the A. nigrescens and 6% of the S. africanus trees examined. This occurrence of nesting holes in a high percentage of C. imberbe could thus be the factor determining this preference.

The average dimensions of the nest holes used are given in Table 27 with the range of size used. The basic nest of the oxpecker is a natural hole in a tree, 1 - 15 m above ground level. In the Satara area, oxpeckers nested in natural cavities where no excavation was required. The average nest

Plate 12. A nest of the red-billed oxpecker (indicated by the arrow) in an _Acacia nigrescens_ tree in the Satara area, December 1974.

Plate 13. A nest of the red-billed oxpecker (indicated by the arrow) in a _Combretum imberbe_ tree in the Satara area, February 1974.

Plate 14. A nest of the red-billed oxpecker (indicated by the arrow) in a _Combretum imberbe_ tree in the Satara area, January 1974.

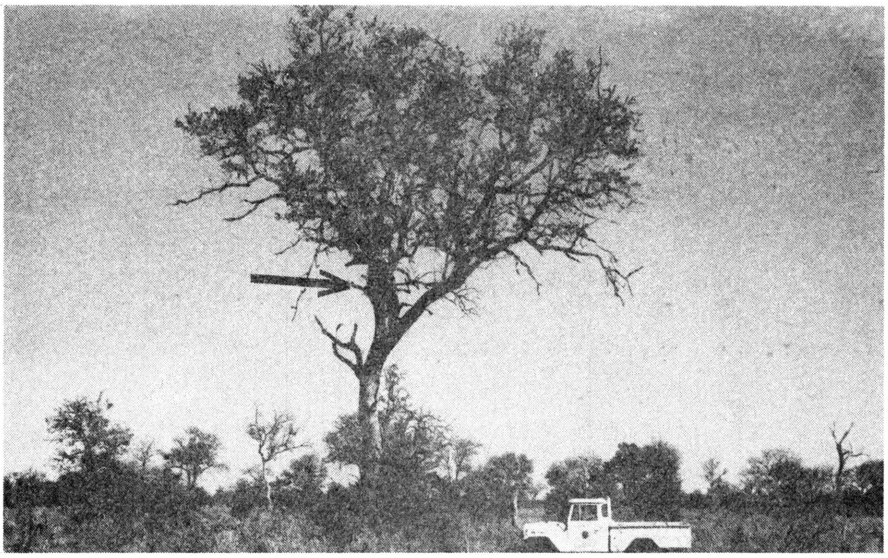


Table 26 : The number of trees large enough* to contain a red-billed oxpecker nest and the number of large enough nest holes in a 16 ha area of the Satara experimental plots in the 1973/74 breeding season.

Tree species	Number counted	Percentage of total	Percentage with nests
Combretum imberbe	10	8	50
Acacia nigrescens	55	43	14
Spirostachys africanus	48	38	6
Guibourtia conjugata	6	6	0
Cassia abbreviata	5	5	0
Total	126		
Range		5-43	0-50

* A tree higher than 2 m and with a main trunk with a circumference of at least 50 cm.

Table 27 : Mean dimensions of 43 red-billed oxpecker nests examined in the Kruger National Park in the 1973/74 and 1974/75 breeding seasons.

Tree species	Height of nest entrance from ground (cm)	Maximum width of nest chamber (cm)	Depth of nest floor below lip of entrance (cm)	Height of entrance hole (cm)	Width of entrance hole at widest point (cm)	Circumference of nesting branch (cm)	Height of nesting tree (m)	Number measured
Combretum imberbe	8,63	12,69	36,97	8,61	7,46	81,51	13,86	36
Acacia nigrescens	4,3	13,0	44,5	7,5	27,0	306,75	5,75	4
Spirotachys africanus	8	15	22	5	10	149	19	1
Kigelia pinnata	13	-	48	7	8	48	15	1
Colophospernum mopane	8	13	28	9	7	84	14	1
Mean dimensions	8,1	14,3	35,9	8,5	[illegible]	103,8	14,7	
Range	1,2-15	9-17	17-81	3,5-20	4 [illegible]	48-1002	2-23	

height above ground level was 8,1 m with a range of 1,2 - 15 m (n = 43, SD = 3,18). The average distance from the hole entrance to the back wall was 35,9 cm, with a range of 17 - 81 cm (n = 42, SD = 18,37) (Table 27).

The direction the nest entrances were facing is given in Appendix 3. The directions expressed as a percentage of the total are the following:

East	5%
North	16%
North-east	12%
North-west	5%
South	12%
South-west	5%
South-east	8%
Vertical	32%
West	12%

A one-way analysis of variance showed that there was a significant difference (F0,05 = 1,94 < 4,2) in the direction the nest entrances were facing. The tendency to nest in natural cavities, relates to the fact that the oxpecker is poorly adapted for digging. Therefore, as the oxpecker breed in natural holes, the direction in which the nest faced is governed by the nature of the nesting hole. It can thus be speculated that there is not enough evidence to prove that the oxpecker prefers nests facing in a specific direction although it appears that there is a preference for nests with a vertical entrance.

Nest occupation

In the Satara area, a total of 21 bird species utilise natural cavities in trees for breeding purposes (Kemp 1972). According to Von Haartman (1957) the drawback in hole-nesting birds is the severe inter- and intraspecific competition for nesting holes. Intraspecific competition was not observed in the oxpecker. However, interspecific competition was frequently observed. In the Satara area the main competitors of the oxpecker are Burchell's glossy starling (*Lamprotornis australis*), cape glossy starling (*Lamprotornis nitens*) and the grey-headed sparrow (*Passer diffusus*). It was observed that oxpeckers, when searching for a nesting hole, were chased from a tree by a bird as small as *P. diffusus*. However, when oxpeckers already occupied a nest, they were able to defend the nest against most other species. Only in two cases were nests taken over by other species. In the first instance a *L. australis* took over a nest in the building stage. In the second case a striped kingfisher (*Halcyon chelicuti*) occupied an oxpecker nest containing eggs.

The same natural cavities may be used for breeding purposes every year. As these observations were not made on marked birds it can thus not be deduced whether these birds are the same individuals or another group of birds. Forty per cent of the nests, where the nestlings fledged during the 1973/74 nesting season, were again utilised in the 1974/75 breeding season (excluding nests that were destroyed). Forty per cent of the nests were utilised by other bird species. These species were *L. australis* (50%) and *L. nitens* (50%). Only 20% of these nests were not occupied by any breeding birds. Forty per cent of the nests where predation occurred in the 1973/74 breeding season were again utilised by oxpeckers in the 1974/75 breeding season. However, only 10% of these nests were utilised by other breeding species while 50% of these nests were not occupied by birds for breeding purposes. This interchange of nest holes could indicate a shortage of suitable holes.

According to Kemp (1972) nest holes in the Satara area are destroyed by natural causes at a rate of about 6% per annum. Nest holes were made unsuitable by fire (once) and by rotten wood filling up the nest hole (two instances). This indicates an annual rate of 14% at which oxpecker nests are destroyed, by natural causes. The effect of fire depends on the tree species and the vegetation at the base of the tree.

Fire had no effect on five dead _C. imberbe_ nesting trees but destroyed an _A. nigrescens_ nesting tree where dry branches were strewn around the base of the tree.

Nesting-material

The nesting-material used by the oxpecker is summarised in Table 28. This information is based on the analysis of nesting-material collected at 15 nests. Animal hair, dung, grass and rootlets are the only material used for nest building. The animal hair is collected from the mammalian symbionts. In a total of 11 observations, ten were from impala (91%) and one from a rufous ox kept at Skukuza (9%). In collecting the hair, a bundle of hair is grabbed with the tip of the beak and pulled out with a backward movement of the head. The hair is carried horizontally in the proximal part of the bill. Hair was only observed to be collected from the back and scapular regions of the mammalian symbionts. The impala reacted to the hair plucking with skin-flicking (75%) and nuzzling (25%). The ox did not show any reaction.

Hair collected from the nests was identified as impala (98%) and kudu (2%) - only one nest. The colour of the hair was dominantly rufous except at the one nest with grey kudu hair. In a yellow-billed oxpecker nest in Nigeria, Mundy and Cook (in press) found only white hair although "there are white and black cows in approximately equal number". They speculate that the yellow-billed oxpecker carefully selects the colour of the mammalian hair it uses so that its eggs show up to good advantage in a dark hole. Ingle (1909 _In_: Mundy and Cook in press) found a red-billed oxpecker nest "lined with white and grey cowhairs ..... when most of the herd are black and red cows". Van Someren (1951) found "reddish" hair in a nest of the red-billed oxpecker and Benson (1946) noted white and black hair in another. In the Satara area white hair is available from the belly of impala but no white hair was found in a total of 43 nests. However, it must be easier for the birds to collect hair from the back of a symbiont than from the belly while hanging upside

Table 28 : Nest building-material used by the red-billed oxpeckers at 15 nests in the Satara area in the 1973/74 and 1974/75 breeding seasons.

	Hair		Grass and rootlets			Dung		Total mass of nesting-material collected from each nest
	Mass of total	%	Species	Mass of total	%	Mass of total	%	
	18,0	90	Impala	2,0	10			20,0
	14,0	88	"	3,0	12			17,0
	22,0	93	"	1,7	7			23,7
	19,5	94	"	1,4	6			20,9
	16,5	91	"	1,6	9			18,1
	20,5	85	"	1,3	6	2,4	9	24,2
	15,9	93	"	1,2	7			17,1
	17,4	97	"	0,6	3			18,0
	8,4	80	"	2,1	20			10,5
	33,4	93	"	2,8	7			36,2
	11,7	95	Kudu	0,7	5			12,4
	18,0	94	Impala	1,3	6			19,3
	17,7	96	"	0,9	4			18,6
	19,6	92	"	1,8	8			21,4
	16,0	94	"	1,1	6			17,1
Mean	17,9	93		1,5	7			19,6
Range	8,4-33,4			0,6-3,0				10,5-36,2

down. In addition, in the Satara area the only long soft hair available is from impala and kudu.

A total of 7% of the nesting-material consisted of dry grass and rootlets (Table 28). These were collected from the ground underneath the nest and carried to the nest in the tip of the bill. Grass stems are brought to the nest, one at the time. Oxpeckers were twice observed to collect dry elephant dung for nesting purposes. Dung was only found in one nest and comprised 9% of the total nesting-material. According to Prozesky (1964) the utilisation of animal dung for nesting purposes is common in the Sturnidae but no data is given to support this statement.

Description of the nest

If animal dung is used, the nest is started by filling any holes or cracks with dung. This is followed by lining the nest with grass and rootlets. The nest is then lined with a layer of mammalian hair. This is followed by building a very neat round cup, consisting of only mammalian hair. The average measurements of eight typical nest-cups were as follows:

Internal diameter of cup : 8 cm (Range 6 - 10 cm, SD = 3,46)
Depth of cup : 3 cm (Range 2,5 - 4,5 cm, SD = 2,24)

Nests do not retain their cup-shape once the chicks hatch and start growing. By the time they fledge the walls are trampled. The purpose of the nest-cup could thus only be for the protection of the eggs and very young nestlings in the sense of protection against the hard edges of the nesting chamber, preventing it from rolling away and thermoregulation.

During the nest-building period, three full-day observations were made at the nests of a two-member, three-member and four-member group. The social organisation of the oxpecker is not clearly understood and the word group as used in the text is to describe the birds that regularly attend a specific nest. The results are summarised in Table 29,

Table 29 : A comparison between the nest-building behaviour of three different group sizes of the red-billed oxpecker from results obtained from three full-day observations at three different nests in the Satara area in the 1973/74 breeding seasons.

Number of birds in group	Number of visits				Number of times nesting-material brought to nest	Total time birds present at nest in min	Mean group size visited nest	Standard deviation of mean group size that visited nest
	One bird	Two birds	Three birds	Four birds				
Two-member group	1	25	-	-	29	200	2	0,35
Three-member group	19	11	3	-	12	445	1,5	0,69
Four-member group	0	4	3	1	4	122	2,4	1,27

Figs. 19 and 20. Because of the danger of the birds deserting the nest during nest-building, no birds were marked, with the result that the role of the sexes could not be determined. In addition, these observations were not done during the same stages of nest-building with the result that no comparison could be made between the three different group sizes.

An accurate estimate of total time involved in nest-building could not be made, because the nests were discovered as a result of the building activities already under way. It was also difficult to determine when a particular nest was completed. However, the maximum observation time spent in nest-building was six days. Six bundles of animal hair were collected at the nests and the mean mass calculated as 0,15 g per bundle. As the mean number of times nesting-material was brought to the nest was 15 per day (Table 29) and the mean number of bundles of animal hair needed to build a nest (15 nests) was calculated as 119, the total length of time involved in nest-building may be more than eight days. However, it must be borne in mind that nest-building continues throughout incubation and the nestling-period. This could have had an influence on the correctness of the calculated length of the nest-building period. Moreover, this could also be the reason why the calculated length of the nest-building period is two days longer than the observed length of the nest-building period. According to Allen (1961) most passerine birds require about six days for nest-building but the length of time is also subject to wide interspecific and intraspecific variation.

From Figs. 19 and 20 it is clear that the greatest activity in nest-building occurs between 05h00 and 11h00. A test on the coefficient of correlation showed a significant relationship (t-test, $P < 0,05$) between the nest-building activity of the oxpeckers and ambient temperature. The reason for this is unknown, but it could be related to the thermoregulatory behaviour of the oxpeckers (see section under thermoregulatory behaviour). Further, nest-building was interrupted by rain and a bird was observed to stay in the nest chamber during the rain. The bird reappeared only

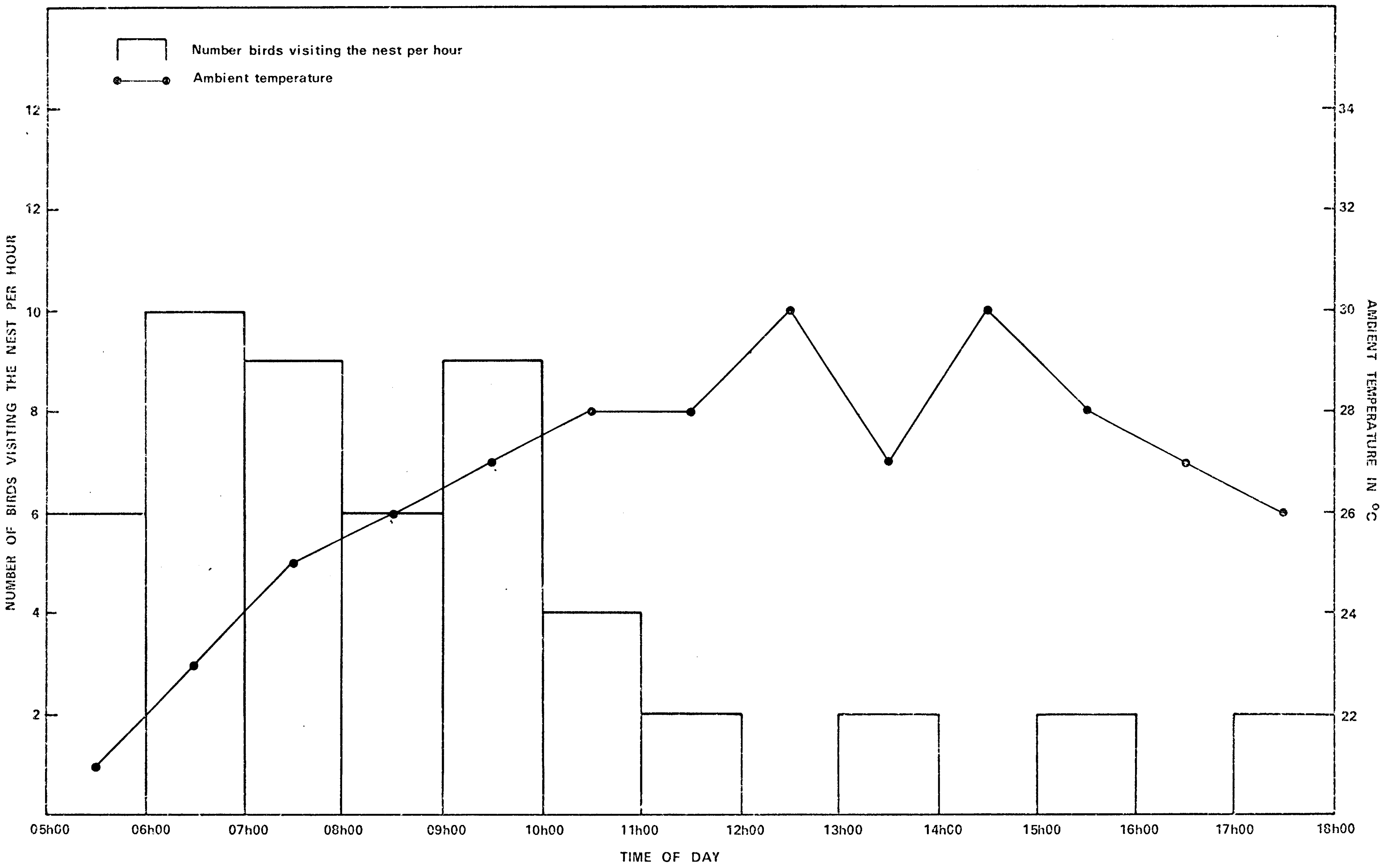


Fig. 19. Number of birds visiting a nest per hour during the nest-building period in a three-member group of the red-billed oxpecker in the Satara area in the 1973/74 breeding season.

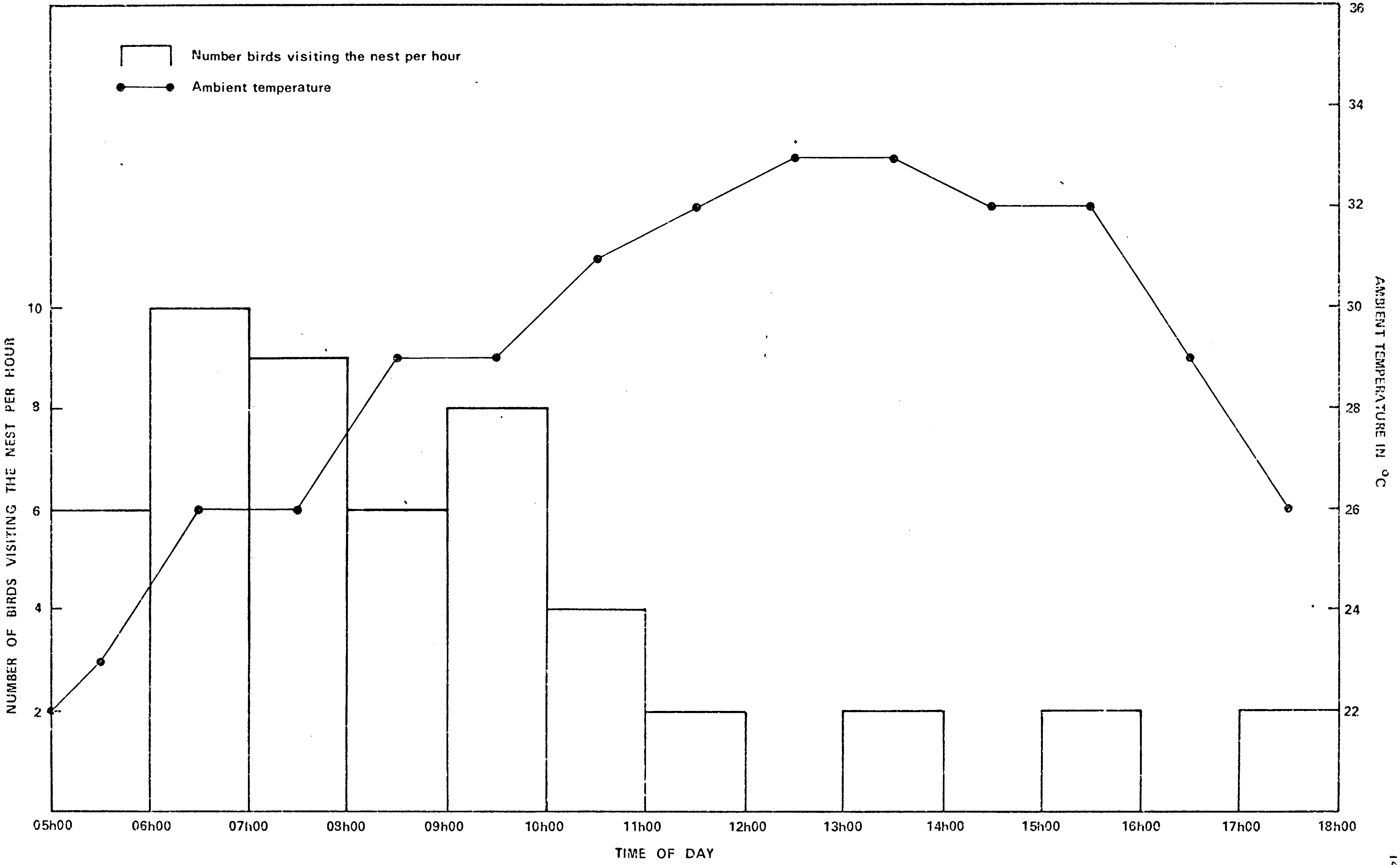


Fig. 20. Number of birds visiting a nest per hour during the nest-building period in a two-member group of the red-billed oxpecker in the Satara area in the 1973/74 breeding season

after the weather cleared. During the nest-building period no birds stayed at the nest during the night.

During incubation, from a total of 140 h of observation, nesting-material was taken 12 times to the nest. Moreover, at a nest of a five-member group during incubation, nesting-material was only bought to the nest in the first four days of incubation. During the nestling period, from a total of 126 h of observation, nesting-material was only observed to be taken twice to the nest. Nest-building thus continues throughout incubation with decreasing frequency, and stops almost completely when the young hatch. It can be speculated that the practice of adding the lining during incubation reduces the number of special visits necessary to build the nest and even the average amount of work the group must do in building those nests.

All the birds in the group collect nesting-material. In the two-member group, in 64% of the visits, both birds brought nesting-material to the nest. In the three- and four-member groups the whole group brought nesting-material to the nest in only 14% and 9% of the visits respectively (Table 29). No correlation was found between the total mass of nesting-material and the size of the group (t-test, P>0,05). As the nest-cup is rebuilt after every breeding session, the number of breeding sessions in the breeding season, must have an effect on the mass of the nesting-material. Predation could also effect the mass of the nesting-material as the birds desert the nest following predation.

No account can be given of the actual process of nest-building, as it was impossible to observe the birds after they had entered the nest. The wing-flapping and the open-wing display were frequently observed during nest-building. The wing-flapping display was usually given when a bird disappeared or reappeared in the nest entrance. During nest-building only one bird at a time entered the nest. As the whole group brings nesting-material to the nest and all the birds with nesting-material enter the nest, it can be speculated that the whole group participated in the process of nest-building.

The eggs

Description of eggs

All the eggs examined corresponded closely to the description given in Winterbottom (1971), tending to be white or pinkish white, with small spots of red-brown, purple and lilac. Pale or unspotted eggs are known to be of adaptive value for a hole-nester, enabling the incubating bird to see its eggs more easily in a dark nest (Von Haartman 1957), however, both species of oxpeckers lay spotted eggs. This rule of egg colour has many exceptions and is probably related to the taxonomic position of the species concerned.

The average of 18 eggs measured was 24,8 x 17,0 mm; the range was 23,7 - 26,5 x 16,2 - 17,6 mm. McLachlan and Liversidge (1970) give the average measurement of 24 eggs as 23,3 x 17,2 (22,5 - 25,5 x 15,8 - 18,5) mm.

Clutch size

According to Pettingill (1970) a clutch of eggs is the total number of eggs laid by one bird in one nesting. Winterbottom (1971) gives the clutch size of the red-billed oxpecker as 2 - 5 with "most often" 2 or 3 eggs. The average clutch size in the study area during the two breeding seasons was 2,8 (SD = 0,62, n = 35). The average clutch size during the 1973/74 breeding season was 2,8 (SD = 0,85, n = 27) and during the 1974/75 breeding season 2,6 (SD = 0,61, n = 8). Because of the small sample in the 1974/75 breeding season no comparison can be made between the 1973/74 and 1974/75 breeding seasons.

Table 30 indicates that 65% of the clutches consisted of three eggs and 23% of two eggs. Only two records of a four-egg clutch, one record of a one-egg and one of a five-egg clutch were found (Table 30). In an analysis of the coefficient of correlation, no significant relationship (t-test, P> 0,05) was found between the size of the group and clutch size (Table 31). Moreover, in a two-way analysis

Table 30 : Frequency of different clutch sizes of the red-billed oxpecker in the Satara area in the 1973/74 and 1974/75 breeding seasons.

No. of eggs in clutch	1	2	3	4	5
No. of records	1	8	23	2	1
Percentage	3	23	65	6	3

Table 31 : Clutch sizes as related with the different group sizes of the red-billed oxpecker in the Satara area in the 1973/74 breeding season.

Size of group	Mean clutch size	Mean size of different clutches			Number of clutches
		First	Second	Third	
2	3	3	3	3	6
3	2,6	2,5	3	2	8
4	3,4	3,2	4	3	8
5	2,7	3	2,5	3	4

of variance earlier clutches did not differ significantly ($F0,05 = 5,14 > 4,11$) from later ones, nor did second or third clutches differ significantly in size from the first. However, this could be a bias originating from the small sample.

Egg-laying

According to Pettingill (1970) birds usually lay very early in the morning. Seel (1966) found that Passer domesticus laid its eggs between about ½ and 1½ h after sunrise throughout the breeding season. Although the exact time of egg-laying was not observed in the oxpecker, the eggs are laid before 09h00. One egg is laid every morning (every twenty-four hours) until the clutch is complete. It is not known if the female enters the nest the evening before or the morning of the start of egg-laying. Oxpeckers are determinated egg-layers e.g. they lay a definite number of eggs per clutch. If the eggs are removed, the birds desert the nest after they have laid the normal number. Furthermore, if an egg is broken or removed during the egg-laying period or after the clutch is completed, this egg is not replaced.

The eggs are laid when the nest-cup is completed. At one nest, however, two eggs (the complete clutch) were laid before any nesting-material was brought into the nest. Four days later the nest was completed. Incubation at this nest did not start before the nest was completed. At another nest three eggs were laid five days after the chicks hatched. This occurred at a four-member group nest and could have been the result of another female laying in the nest.

Incubation

The incubation rhythm

The red-billed oxpecker begins to sit on the nest after laying the first egg. According to Pettingill (1970) a bird sitting on its nest before the clutch is complete, may or may not involve fully warming the eggs. Thus its presence on the nest may not always indicate that incubation has actually begun. Incubation actually commences only when the bird applies maximum body heat to the eggs; this was not determined in the oxpecker. However, as hatching was asynchronous it appears that incubation started after the first egg was laid. From six nests in which both the laying dates and hatching dates were known, the mean incubation period from the day when the last egg was laid to the day when the last chick hatched was 12,6 days with a range of 12 - 13 days, compared with 11 - 12 days given by McLachlan and Liversidge (1970).

A total of ten full-day observations were made during the incubation period in the Satara study area. These results are summarised in Tables 32 and 33. Only at one nest (a five-member group) were observations made on colour marked birds. These birds were collected after the study period for identification. From observations at this nest it became clear that only one female and one male (the active male and female) participate in incubation, although the other birds in the family group were frequently observed at the nest.

In this group both the active male and female were in active breeding conditions indicated by an enlarged ovary or testis.

The active female was observed to incubate the eggs at night, but was frequently relieved by the active male during the day-time period. In one observation the active male incubated the eggs for 385 min (59%) of the time between 05h00 and 19h00 while the active female was attentive for only 267 min (41%). The active female was relieved at the nest for the first time between 05h00 and 05h30. For the night incubation period, the incubating female settled on the eggs before 18h30.

The mean number of change-overs of incubating birds were calculated as 1,0 per h from a total of 140 h of observation. From Table 33 it is clear that there is a gradual decrease in the number of change-overs per hour as the day progresses. A test on the coefficient of correlation showed

Table 32 : The incubation rhythm of the red-billed oxpecker obtained from ten full-day observations at different nests in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Mean ambient temperature in °C	Number birds in group	Days after first egg laid	Number of times incubating birds were relieved at nest in a 14 h period	Total time no birds were present at nest in a 14 h period in min	Total number of birds visiting nest	Number times nesting-material was brought to nest	Number juvenile* birds in group
27	2	3	12	82	15	0	3
34	2	5	14	54	21	2	1
24	3	3	12	49	16	1	0
30	4	3	12	37	17	0	0
33	4	4	11	99	22	1	0
29	4	11	24	232	37	4	0
29	5	3	20	83	31	2	1
24	5	4	20	63	38	2	0
36	5	6	11	99	14	0	0
31	5	11	13	87	23	0	0
Mean			14,9	88,5	23,4	1,2	
Range			11-24	37-232	14-38	0-4	
SD			13,96	164,14	26,80	3,94	

Table 33 : Number of change-overs in the incubating red-billed oxpecker in the Satara area in the 1973/74 and 1974/75 breeding seasons as observed at ten different nests.

Hour of day	5-7	7-9	9-11	11-13	13-15	15-17	17-19
	Number of change-overs in incubating birds						
	3	2	4	1	2	0	2
	2	2	2	2	0	1	3
	2	2	3	2	1	1	1
	3	2	1	1	1	1	1
	4	5	2	6	4	2	1
	3	4	4	3	3	1	2
	2	4	2	3	4	3	2
	2	2	1	1	3	1	1
	2	4	2	0	2	2	1
	2	3	1	2	2	1	1
Mean	2,5	3,0	2,0	2,1	2,2	1,3	1,5
Range	2-4	2-5	1-4	0-6	0-4	0-3	1-3
SD	2,12	3,46	4,47	4,98	3,95	2,47	2,12

no significant relationship (t-test, $P > 0,05$) between the mean ambient temperature and the number of change-overs per day. Moreover, no significant correlation (t-test, $P > 0,05$) was found between the number of birds in the group and the number of change-overs per day (Table 32).

The incubation rhythm is summarised in Tables 32 and 33. The average time the birds were absent from the nest between 05h00 and 19h00 was 88 min. The high percentage of attentiveness (92%) is possible because the male shares incubation. A test on the coefficient of correlation showed no significant relationship (t-test, $P > 0,05$) between the mean ambient temperature and the time spent off the nest during the day (inattentive period) (Table 32). The percentage of inattentiveness shows stability for most of the day but increases during nightfall (Fig. 21).

During incubation the average number of times nesting-material was brought to the nest was 1,2 times per day ($n = 10$, $SD = 3,94$) (Table 32). Both the active male and female were observed to bring nesting-material to the nest.

According to Von Haartman (1957) an adaptation of hole-nesting birds is hissing by incubating birds when disturbed but give no reason why. Mundy and Cook (in press) observed this behaviour at a yellow-billed oxpecker nest in Nigeria. They were also able to catch an adult bird sitting on the nest. This hissing was only once observed in an adult red-billed oxpecker which was brooding chicks, on a cold, wet day. When a human approached a nest containing an incubating bird, the bird would quietly slip off the nest and would fly away or go and sit in a nearby tree. Only when away from the nest would the bird give the alarm call.

Nest relief was fairly simple. The approaching bird would give the contact call which was answered by the incubating bird coming out of the nest. The one bird would then enter the nest while the other bird would fly away. The wing-flapping display and the open-wing display were observed at the nest during the incubation period. The incubating bird

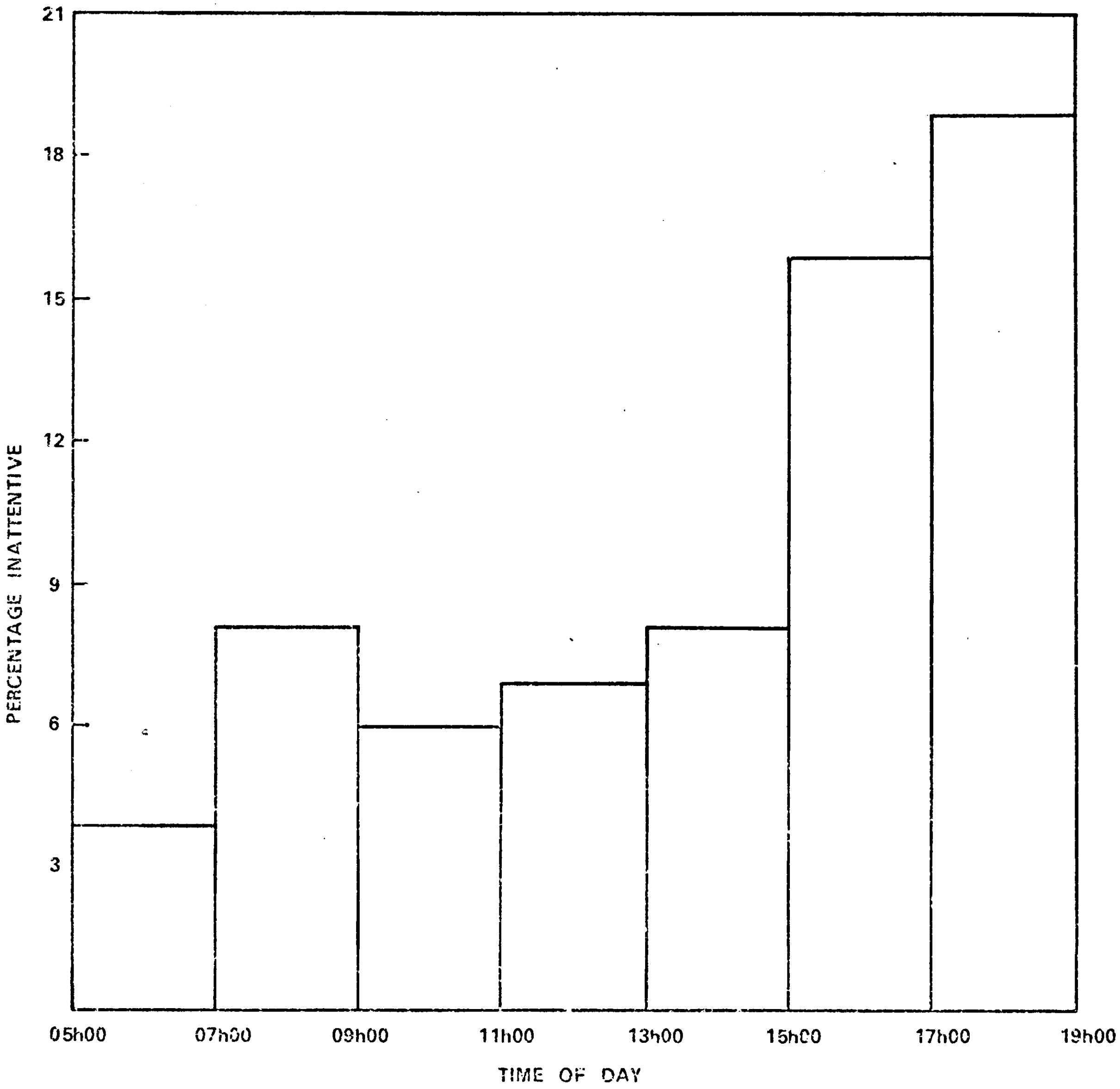


Fig. 21. Percentage inattentiveness as related with time of day in incubating red-billed oxpeckers observed at ten different nests in the Satara area in the 1973/74 and 1974/75 breeding season.

was also observed to sit in the nest entrance, preening itself. Defaecation by the incubating birds always occurred away from the nest.

Hatching of eggs

According to Skutch (1952) the hour of hatching in a single species or in a single nest is usually far more variable than the hour of laying. The time of day at which hatching took place was observed three times in the red-billed oxpecker e.g., 09h00, 11h40 and 14h00. It seems, therefore, that hatching can take place at any time of the day. No broken eggshells were observed in any nests although some nests were visited soon after hatching. In addition, no broken eggshells were found underneath the nests. It is thus apparent that the eggshells are removed from the nest shortly after hatching. The advantage in removing shells to some distance from the nest before dropping them could be to get rid of conspicuous objects that could attract predators to the immediate vicinity of the nest.

Fourteen hours of observation were made at a three-member group nest during hatching of the chicks. The nest contained two eggs and a chick that had hatched the previous night. The chick was fed four times only during the observation period and only in the afternoon. The adult birds brooded the chick for 88% (740 min) of the day-time period. A total of 34 birds visited the nest and the adult birds were changed 33 times.

Another 14 hour observation period was carried out at the same nest after all three chicks had hatched and the oldest chick was about three days old. During this observation period, a total of 41 adult birds visited the nest and the chicks were fed 36 times. The adult birds brooded the chicks for 64% (545 min) of the day-time period. This shows a significant decrease ($Z0,025 = \pm 1,96 < 11,5$) in the time the chicks were brooded. The reason for this could be that during the hatching period the remaining eggs are incubated and it is not necessary the chicks that are brooded. No brooding was observed during the day-time period at a nest with chicks that were about eight days old. However, there was always an adult bird with the chicks during the night.

Hatching success

The hatching success was calculated from only those nests from which the complete clutch and the number of newly hatched young were known. Predation was not taken into account in the calculation of hatching success. During the 1973/74 breeding season, 46 chicks hatched from a total of 64 eggs which gives a hatching success of 72%. Table 34 gives the hatching success as related to the size of the group. No significant difference (t-test, $P > 0,05$) in the hatching success was found for the different group sizes.

The nestling period

Care of the young

When the eggs had hatched the attitude of the other birds in the group changed. Once they discovered that there were nestlings, they started to assist the active male and female in feeding them. Compared to the incubation period, the average number of birds that visited the nest increased from 23 per day to 57 per day (Table 35). In a total of nine full-day observations, nesting material was only brought twice to the nest compared to 12 times in about the same observation period during incubation.

The food was carried in the mouth and was not regurgitated. An adult bird with food was easily identified by the bulgy cheeks. Feeding rates, from 126 h of observation at nests are recorded in Tables 35 and 36. From these figures the feeding rate of the oxpecker can be calculated as 3,1 feeds per hour ($n = 393$, $SD = 3,52$). Considerable variation exists, from 0,3 - 4,7 feeds per hour. However, if the number of chicks is taken into consideration, the feeding rate of the oxpecker can be calculated as 1,4 feeds per chick per hour ($n = 393$, $SD = 3,87$). These results can be compared

Table 34 : Hatching success as related to the size of the group in the red-billed oxpecker in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Size of group	Number eggs	Number hatched	Percentage hatched
2	15	10	67
3	11	8	73
4	23	18	78
5	13	8	62
Mean	64	46	72
Range			62-78
SD			31,46

Table 35 : Care of the nestlings of the red-billed oxpecker obtained from nine 14 h observations at different nests in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Number of adult birds in group	Age of oldest chick in days	Number of chicks	Total number birds visited nest	Number times chicks were fed	Attentive period in min	Mean ambient temperature in °C	Number of times nesting material was brought to nest	Number of juvenile* birds in group	Mean number of feeds per hour
3	hatching	1	34	4	840	34	0	0	0,3
3	3	3	41	36	545	33	1	0	2,5
4	14	4	58	48	62	22	0	0	3,4
4	17	2	73	64	269	28	0	0	4,5
4	31	3	52	41	435	28	0	0	2,9
5	8	2	71	47	206	31	0	0	3,4
5	13	2	59	45	294	31	1	1	3,2
5	15	2	45	41	75	24	0	1	2,9
5	17	2	82	67	132	27	0	1	4,7
Mean			57	43	317				3,1
Range			34-82	4-67	62-840				0,3-4,7
SD			47,58	56,18	718,04				3,52

* A fledgling of a previous brood of the same breeding season.

Table 36 : Feeding rate of chicks observed at different nests of the red-billed oxpecker related with time of day in the Satara area in the 1973/74 and 1974/75 breeding seasons from a total of 126 h of observation.

Number of adult birds in group	Age of oldest chick	Number of chicks	Number of feedings correlated with time of day						
			5-7	7-9	9-11	11-13	13-15	15-17	17-19
3	1	hatching	0	0	0	1	1	1	1
3	3	3	2	6	4	2	7	7	7
4	14	4	9	7	6	4	7	7	8
4	17	2	10	11	11	10	7	7	2
4	31	3	7	6	7	5	3	8	8
5	8	2	6	7	7	7	10	4	6
5	13	2	4	6	7	11	8	3	6
5	15	2	1	7	10	5	12	4	2
5	17	2	13	13	11	13	3	11	3
Mean			5	7	7	6	6	6	4
Range			0-13	0-13	0-11	1-13	1-12	1-11	1-8

to those of Rowley (1965) in the superb blue wren (Malurus cyaneus)(also a co-operative breeder), with a observed mean feeding rate of 5,8 feeds per chick per hour.

According to Pettingill (1970) the rate of feeding in passerine species increases daily because of the increasing needs of fast-growing young. A test on the coefficient of correlation showed a significant relationship (t-test, $P < 0,05$) in the oxpecker between the rate of feeding and the age of the chick. Moreover, with a positive correlation, the feeding rate increase with an increase in the age of the chick. A significant relationship (t-test, $P < 0,05$) was also found between the feeding rate and the number of adult birds in the group that attend a given nest (Fig. 22). No significant relationship (t-test, $P > 0,05$) was found between the number of chicks and the feeding rate in the oxpecker. Nice (1943) has found that those species that customarily carry only one item of food per trip, increase the rate of feeding by making more trips, whereas, those species that carry several items of food, increase the rate of feeding by supplying greater amounts of food per trip. Although no information is available on the size of individual food items and of the number of items or objects per feed, the oxpecker could also increase the rate of feeding by supplying greater amounts of food per trip. With an increase in the feeding rate with an increase in the age of the chick, however, it appears that the oxpecker does not increase the amount of food per trip, but increases the number of trips to the nest. According to Seel (1970) the limit to the visiting frequency is in fact an adaptation directed towards obtaining the maximum amount of food. If the food items occur in groups of limited size (ectoparasites on a group of mammalian symbionts), attracting the attention of other birds by very frequent journeys may be disadvantageous. The maximum visiting frequency of the oxpecker may therefore represent a balance between the advantage of bringing more food and the disadvantage of attracting the attention of other parents to such food or attracting predators to the nest.

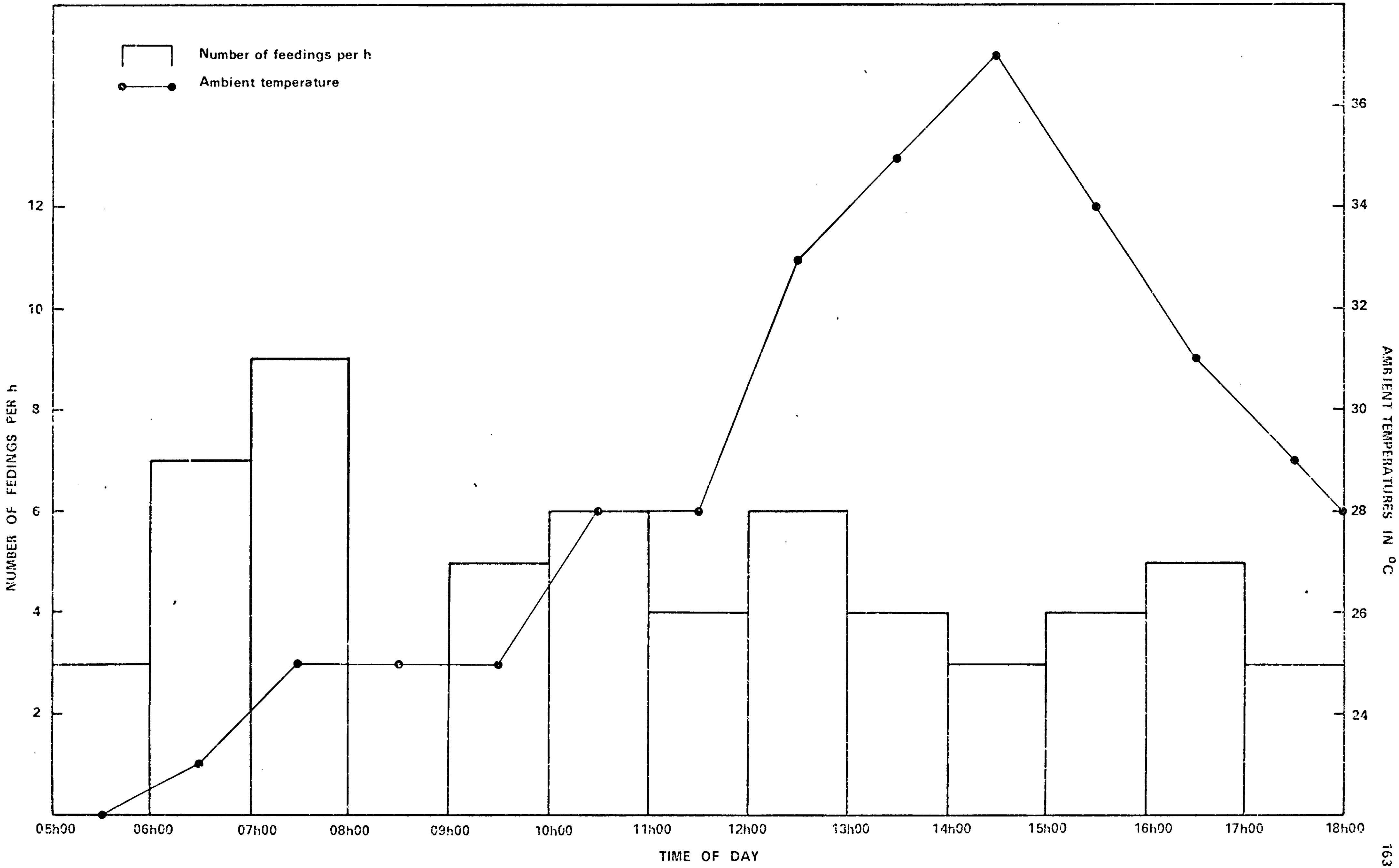


Fig. 22. Number of times 17 day old chicks were fed by a four-member group of the red-billed oxpecker in the Satara area in the 1974/75 breeding season

The figures in Table 36/ Figs. 22 and 23 indicate that the feeding rate during the day was fairly constant except for a slight peak between 06h00 - 08h00. A test on the coefficient of correlation showed no significant relationship (t-test, P > 0,05) between the feeding rate during the day and the mean ambient temperature. Table 35 shows that the mean attentive period during the active daytime cycle was 317 min. This is 38% of the total daytime period (05h00-19h00). A significant relationship (t-test, P< 0,05) was found between the mean ambient temperature and the time the birds were attentive at the nest. This is probably related to the thermoregulatory behaviour of the birds. The relationship between the total number of birds that visited nine different nests in a 14 h period and the mean number of feeds per hour as observed in the Satara area during the 1973/74 and 1974/75 breeding seasons,is shown in Table 36. These results were plotted in quest of any discernable correlation (Fig. 24). When these two variables were further analysed a statistically significant correlation (t-test, P< 0,05) was found between the total number of birds that visited a nest in a 14 h period and the mean number of feeds per hour. This relationship is demonstrated with a straight line regression in Fig. 24.

The food for the nestlings is collected on the symbionts by plucking and in a few cases by insect catching. Scissoring is not used because it would be impossible for the birds to scissor with food already collected in the bill. From observations, oxpeckers do not appear to have any difficulty in collecting food for their nestlings. An adult bird was observed to fly from the nest to a warthog standing about 50 m from the nest. This bird returned to the nest with a food load, in 158 sec after leaving the nest.

Nest sanitation

In the nestlings, defaecation often occurs immediately after feeding, in the form of a faecal sac. The adults collected these sacs, following a feeding, and carried them

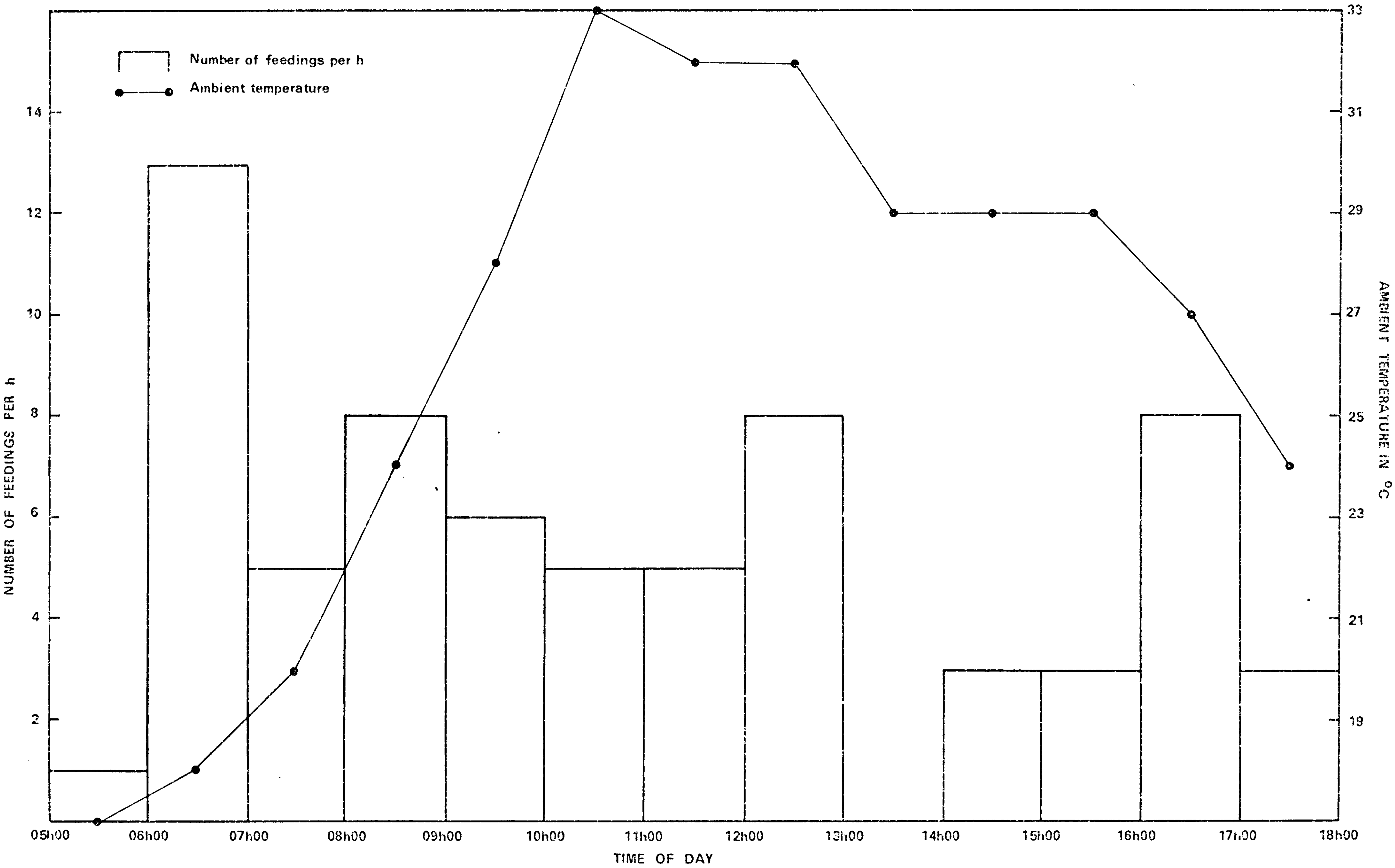


Fig. 23. Number of times 17 day old chicks were fed by a five-member group of the red-billed oxpecker in the Satara area during the 1974/75 breeding season.

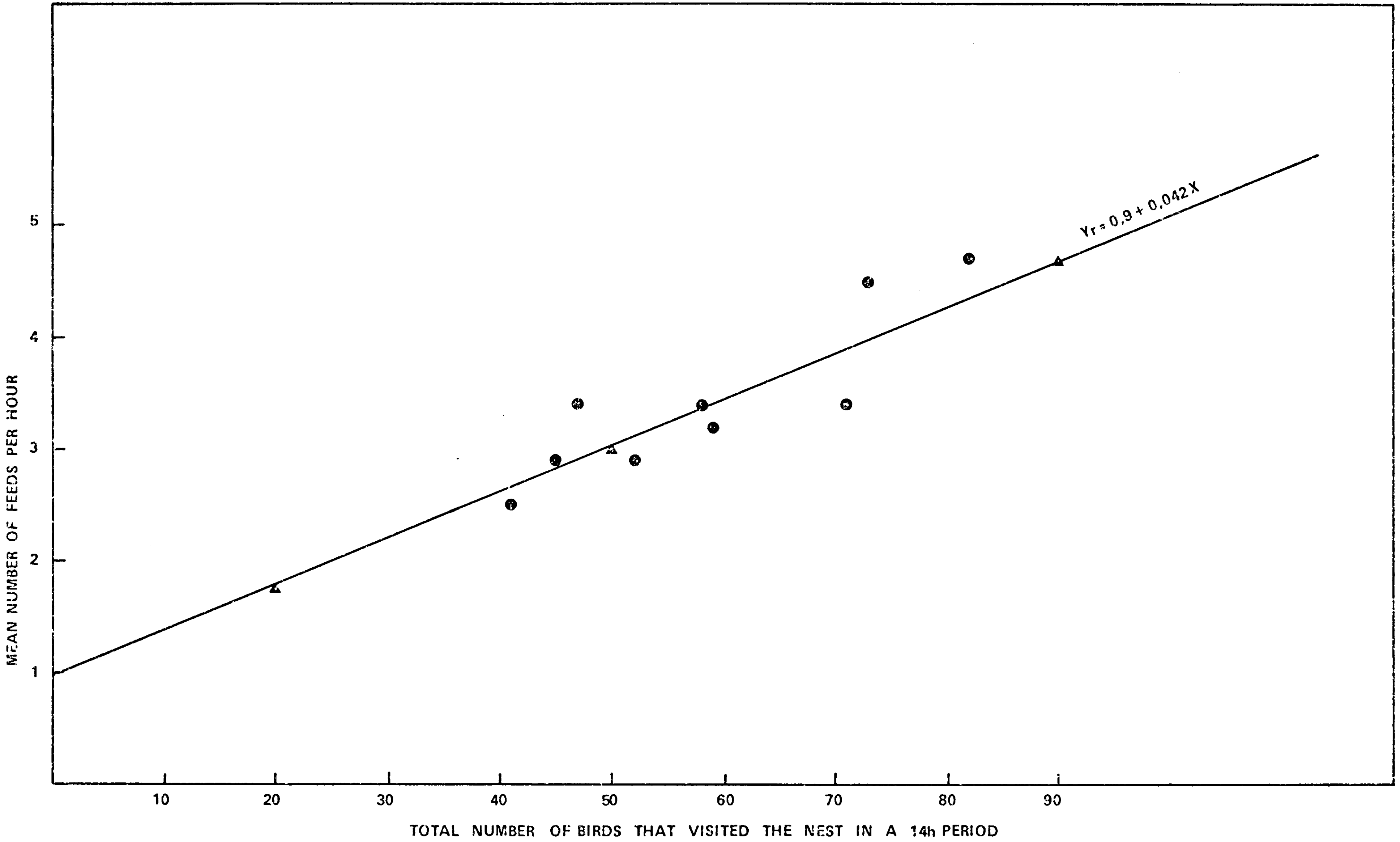


Fig. 24. The relationship between the total number of birds that visited nine different nests in a 14 h period and the mean number of feeds per hour as observed in the Satara area during the 1973/74 breeding seasons.

away and dropping them while in flight. From a total of 11 observations the mean distance these faecal sacs were carried from the nest, was calculated as 31 m (SD = 15,8). After dropping the faecal sacs, 52% of the birds returned to the nest for bill-wiping. Although the birds collected faecal sacs following a feeding they did not necessarily collect them after every feeding. The percentage of times the excreta were removed (in terms of number of feeding trips) was 19% (Fig. 25). From this, the mean feeding/defaecation rate can be calculated as 4,7. However, the number of faecal sacs increased as the young grew older and decreased again just before the nestlings fledged. The feeding/defaecation ratio differs thus for nestlings of different ages. The adults continued to carry away faecal sacs until the day the young left the nest. Any faecal sacs dropped outside the nest were also removed by the adult birds. Rand (1942) conducted experiments with artificial faecal sacs at the nests of the song sparrow (Melospiza melodia). He concluded that the voiding of the young provided no special stimuli to the nest-sanitation behaviour of the adult, but the presence of the young was necessary for nest sanitation to be carried out. In addition, the nest-sanitation behaviour, the removal of material from the nest, appeared to be complementary to the action of bringing food to the nest.

Oxpeckers were observed to remove any "foreign objects" other than nesting-material from the nest and the nest was kept clean throughout the chicks nestling period. The adults also removed coloured neckbands that were tied around the necks of the chicks during food collecting experiments. In two cases, chicks were carried away and dropped in the same manner as a faecal sac. Broekhuysen (1963) found in his study on the orange-breasted sunbird (Anthobaphes violacea) that the "removal of foreign object" behaviour is activated at a very early stage, even before eggs have been laid. It could thus be in the oxpecker, that faeces are considered a "foreign object" and removed from the nest.

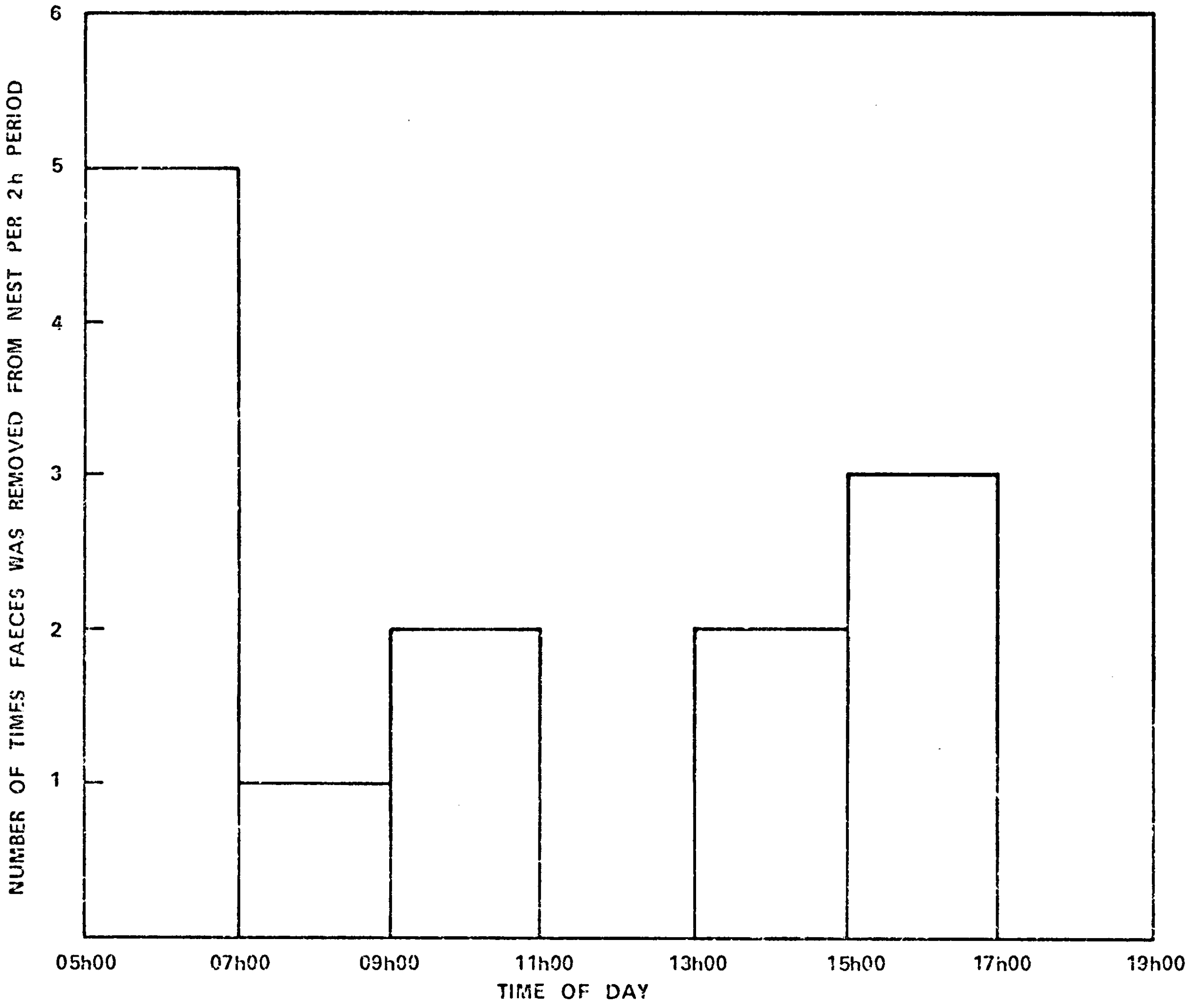


Fig. 25. Removal of faeces at a nest containing four 14 day old chicks of the red-billed oxpecker in the Satara area in the 1973/74 breeding season.

Behaviour of the sexes during the nestling period

The information on the behaviour of the sexes during the nestling period at the three nests, where the adult birds were colour marked, is given in Tables 37, 38 and 39. These results show that up to five birds regularly attend a given nest. This probably results from a substantial non-breeding population which helps in a more or less permanent capacity in any one season, at the nest of a mated pair. From the sex ratios of the helpers (Table 40), it can be speculated that young birds stay with their parental group for at least a year, over the subsequent breeding season. There is, however, no evidence in the form of marked birds to support this speculation. At one nest during the 1973/74 breeding season a two-member group raised three chicks which were colour ringed. During the 1974/75 breeding season the same nest was used by a five-member group but none of these birds were colour marked. From this it can be speculated that another group took over the nest or that the same pair bred in the nest but that the helpers were other birds than the young of the previous season. If the young do not attend to the nest during the next breeding season there must then be a non-breeding population. However, counts were made of the age ratio after the breeding season and then compared with the breeding success, do not support this speculation (see section under population dynamics). A non-breeding population could also follow or stay in flocks on the large herds, like buffalo. Determining the age ratio on these herds is difficult and is usually not done, and could thus be a reason for the fact that these counts did not show the existance of such a population.

All the members of a group feed the nestlings, gaurd them and later care for the fledglings (Tables 37, 38 and 39). A statistical analysis showed no significant difference $(Z0{,}025 = \pm 1{,}96 > 0{,}89)$ between the total number of visits by the males and females. When these data were further analysed, however, a statistically significant difference

Table 37 : Behaviour of different birds at a nest of the red-billed oxpecker containing two eight day old chicks in the Satara area in the 1974/75 breeding season in a 14 h observation.

Sex/Age	Number of visits to nests	Number of times chicks were fed	Percentage of total visits	Attentive at nest in min	Percentage of total attentive period	Number of faecal sacs carried away	Percentage of total number of faecal sacs carried away
Adult ♀	13	13	19	39	16	3	37
Adult ♂	23	17	34	90	38	2	25
Adult ♀	8	4	11	38	16	2	25
Adult ♂	18	10	26	47	20	0	0
Adult ♂	5	3	7	21	8	1	13
Range	5-23	3-17	7-34	21-90	8-38	0-3	0-37
$\bar{x}$	13,4	9,4	19,4	47	19,6	1,6	20,0
SD	14,60	11,88	21,94	51,67	22,36	2,28	28,07

Table 38 : Behaviour of different birds at a nest of the red-billed oxpecker containing two 15 day old chicks in the Satara area in the 1974/75 breeding season in a 14 h observation.

Age/Sex	Number of visits to nest	Number of times chicks were fed	Percentage of total visits	Attentive at nest in min	Percentage of total attentive period	Number faecal sacs carried away	Percentage of total number of faecal sacs carried away
Adult ♀	15	15	37	30	43	5	62
Adult ♂	4	4	10	4	5	1	12
Adult ♂	10	10	25	24	34	2	26
Adult ♂	6	6	15	7	10	0	0
Adult ♀	5	5	12	5	7	0	0
Range	4-15	4-15	10-37	4-30	5-43	0-5	0-62
$\bar{x}$	8,0	8,2	19,8	14,0	19,8	1,6	20,0
SD	9,05	8,12	22,43	24,21	34,91	4,15	51,61

Table 39 : Behaviour of different birds at a nest of the red-billed oxpecker containing two 17 day old chicks in the Satara area in the 1974/75 breeding season in a 14 h observation period.

Age/Sex	Number of visits to nest	Number of times chicks were fed	Percentage of total visits	Attentive at nest in min	Percentage of total attentive period	Number faecal sacs carried away	Percentage of total number of faecal sacs carried away
Adult ♀	20	20	29	49	41	2	14
Adult ♂	8	7	12	12	10	3	21
Adult ♂	20	20	29	28	23	6	42
Adult ♂	12	12	17	24	20	2	14
Adult ♀	8	8	12	7	6	1	9
Range	8-20	7-20	12-29	7-49	6-41	1-6	9-42
$\bar{x}$	13,6	13,4	19,8	24,0	20,0	3,0	20,0
SD	12,13	12,65	17,29	32,77	27,31	3,0	26,04

Table 40 : Sex ratios found in breeding groups of the red-billed oxpecker in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Size of breeding group	Number of males	Number of females	Percentage males	Percentage females
2	1	1	50	50
3	1	2	33	66
5	3	2	60	40
5	3	2	60	40

($Z0,025 = \pm 1,96 < 6,67$) was found in the number of times the active female (breeding female) fed the chicks compared to the other female in the group. Moreover, a significant difference ($Z0,025 = \pm 1,96 < 4,25$) was also found between the number of times the active male (breeding male) fed the chicks compared to the other males in the group, but no significant difference ($Z0,025 = \pm 1,96 > 0,4$), was found in the total number of times the chicks were fed by the active male and female. It can thus be concluded that feeding the young was shared more or less equally by the breeding male and female, with the helpers participating to a lesser extent in all these activities.

The feeding methods used by both sexes were similar. The adult birds arrived at the nest with food, paused, then approached the entrance hole and disappeared into the nest to feed the chicks. No significant difference ($Z0,025 = \pm 1,96 > 1,90$) was found between the attentive period at the nest of the active male and female. Amongst females, the distinction between helper and male was sharp, since never more than one clutch is laid per nest and only one female incubated the eggs. It was, however, not known whether a group built more than one nest. There is no information available that it is the dominant male which necessarily fertilises the female. A statistical analysis showed no significant difference ($Z0,025 = \pm 1,96 > 0$) between the faecal sac removal duties of the active male and female. A significant difference ($Z0,025 = \pm 1,96 < 2,28$) was found, however, between the faecal sac removal duties of the females with the breeding female playing the active role. Moreover, a significant difference ($Z0,025 = \pm 1,96 < 2,0$) was found in the faecal sac removal duties of the males, with the breeding male playing the active part. It can thus be concluded that all the birds share the faecal sac removal duties, but the breeding male and female play the active part.

Development of the chicks

Plumage development

the day old chick.

The chicks of the oxpecker can be described as altricial, nidicolous and psilopaedic i.e. the young at hatching have their eyes closed, are incapable of locomation, remain in the nest for an extended period after hatching, are dependent on their parents for food and are naked at hatching or have only very sparse down on the dorsal region (Plate 15). At hatching, dark grey neossoptiles are present on the occipital region, capital tract, dorsal region and axillar region. Tufts where the rectrices and remiges will appear were also present on the first day. The chicks are pink all over except for a grey colour in the eye region. The viscera were visible through the skin and the egg-tooth was white.

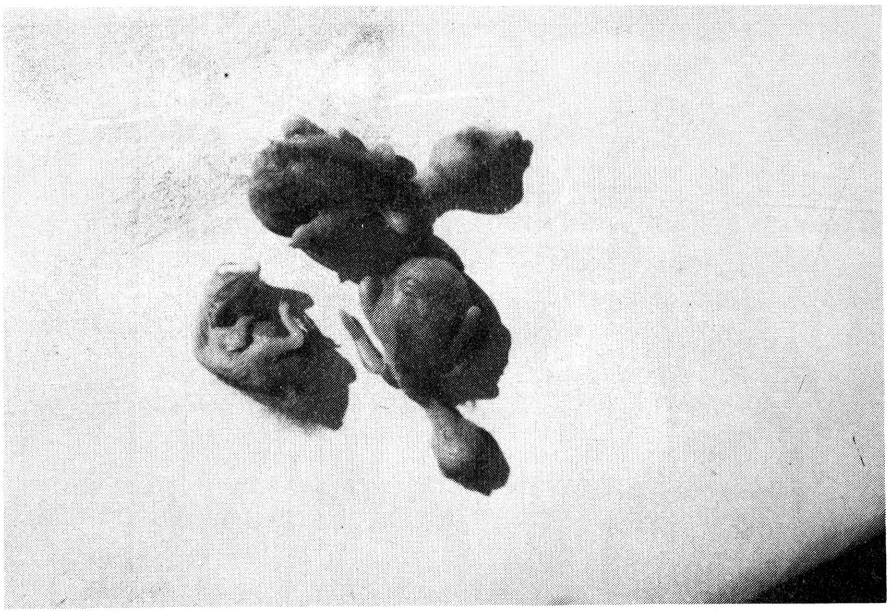
remiges

The growth of the remiges is given in Fig. 26. The quills appeared on day six and the feathers began to break out of the quills on about day eight after hatching. The mean growth rate of the primaries was 3,6 mm per day (n = 8, SD = 4,54). The growth rate of the primaries was calculated from measurements of chicks from five different nests with different brood sizes and with different numbers of adult birds tending the nests. A one-way analysis, however, showed no significant difference ($F0,05 < 5,79$) in the growth rates of the primaries of the chicks from the different nests. Mundy and Cook (in press) have found that the remices and rectrices of the yellow-billed oxpecker grew 3,8 mm and 3,5 mm per day, respectively. In the red-billed oxpecker with the mean length of the adult's first primary as 72,3 mm (n = 19, SD = 39,76) it can be accepted that the primaries were fully grown when the chicks left the nest.

rectrices

The rectrices had the same sequence as the remiges with a growth rate of 3,3 mm per day (Fig. 27). The fledgling's tail was markedly shorter than adult length (95,6 mm) (n = 224, SEM = 0,27). It is apparent that adult length may be reached at the age of 34 d, about five days after fledging, provided the average growth rate is maintained after the

Plate 15. Newly hatched chicks of the red-billed oxpecker in the Satara area, December 1974.



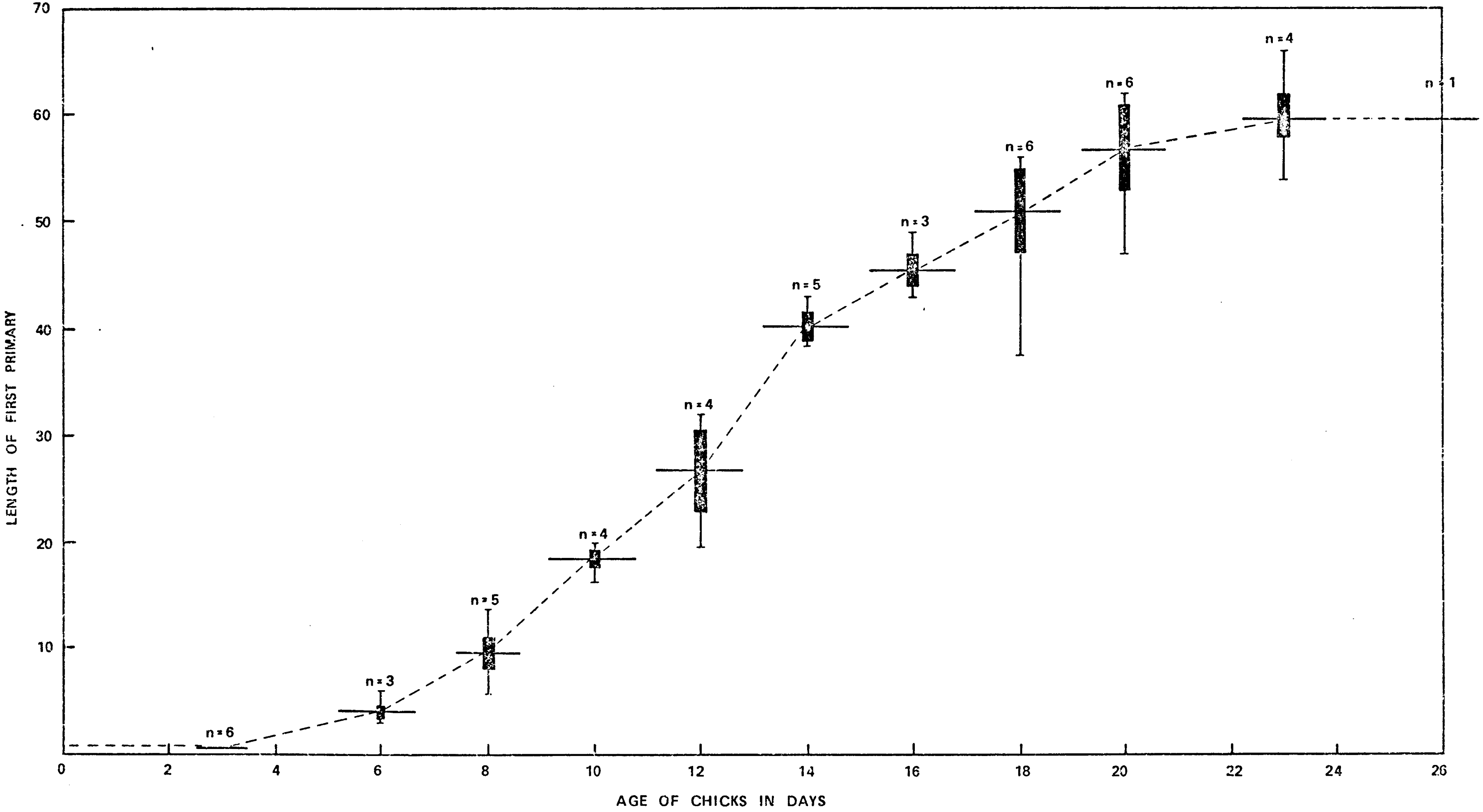


Fig. 26. Average growth curve of the first primary of the red-billed oxpecker chick in the Satara area in the 1973/74 and 1974/75 breeding seasons. Vertical lines represent ranges, vertical rectangles show the standard deviation, and horisontal lines indicate the means

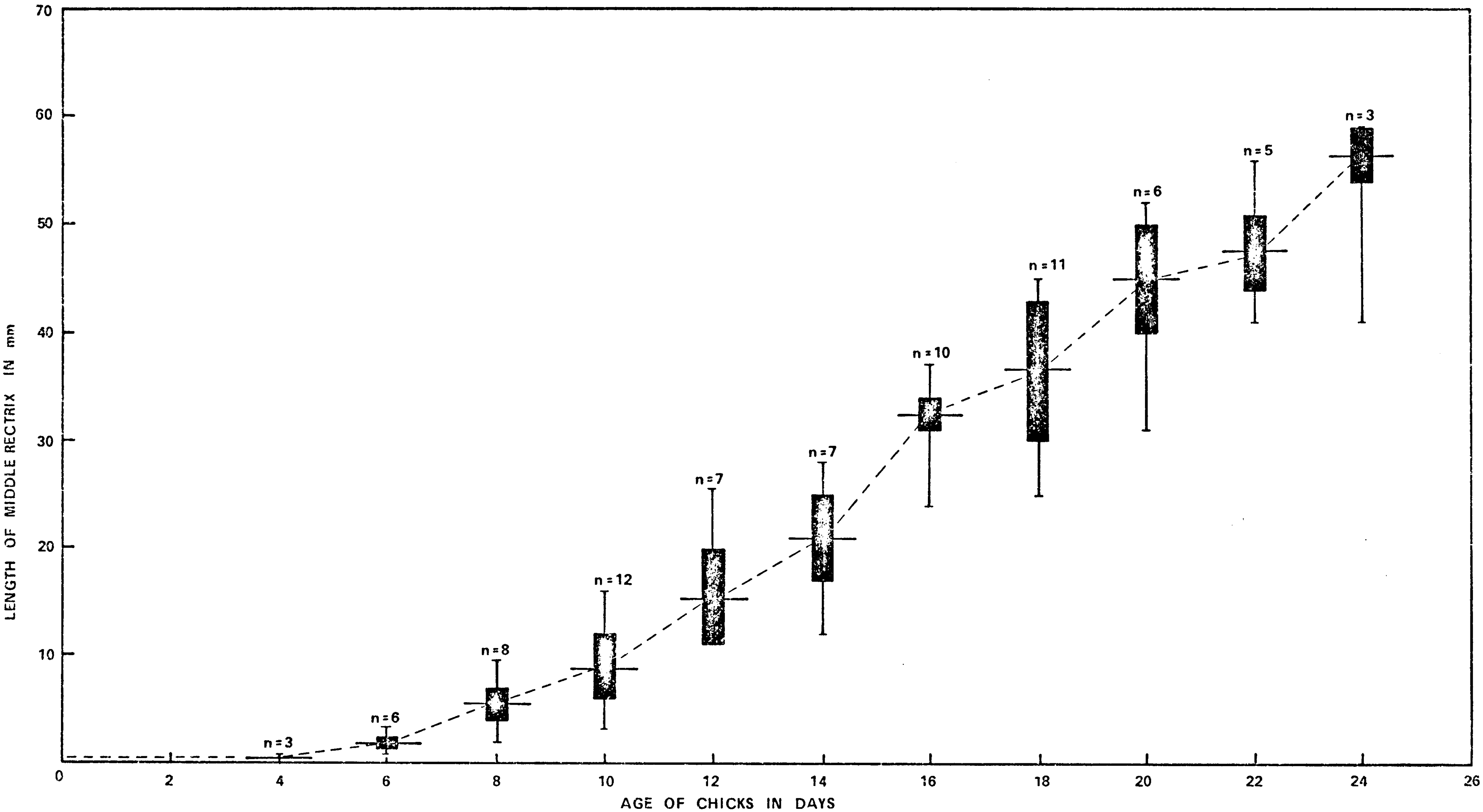


Fig. 27. Average growth curve of the middle rectrix of the red-billed oxpecker chick in the Satara area in the 1973/74 and 1974/75 breeding seasons. Vertical lines represent ranges, vertical rectangles show the standard deviation, and horisontal lines indicate the means.

chick has left the nest. According to Dowsett (1965) the short tail of a yellow-billed oxpecker fledgling is a diagnostic field character. Mundy and Cook (in press) state that adult length in the yellow-billed oxpecker is reached only at the age of 45 days (n = 1).

body areas and wing coverts

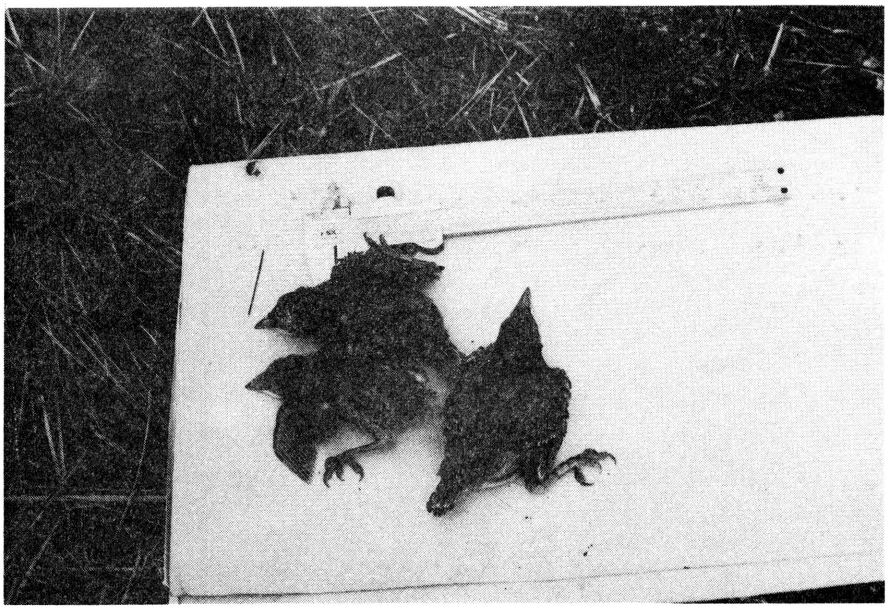
The teleoptiles of the juvenile plumage first showed evidence of development when the feather papillae darken and enlarge on day two. However, on day two only the teleoptiles of the capital tract, spinal tract, humeral tract, femoral tract and the primary and secondary coverts were visible. On day four, the teleoptiles of the coudal tract, ventral tract and the feathers of the alula broke through the skin. The quills of the capital tract, spinal tract, primary and secondary coverts, femoral tract, humeral tract and the ventral tract emerged on day five. The quills of the rest of the body feathers did not emerge before day six. The feathers began to break out of the quills in the same order on day nine (Plate 16). By the time of nest leaving, the teleoptiles were sufficiently lengthened, unfolded and expanded to cover all the apteria (Plate 17). The dorsal teleoptiles of the juvenile plumage were a much darker grey than the adult plumage.

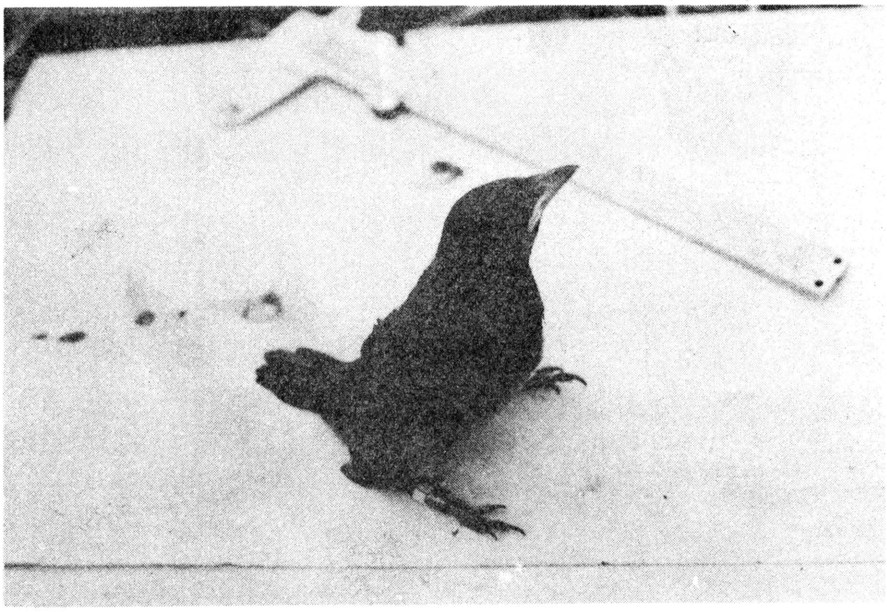
The eyes

The eyes were closed at hatching and the future openings were only visible on the fourth day as a line on the skin. The ridges of the eye-lids were obvious by day five. The wattle around the eye developed from day five and started to darken on the ridges from day seven and was dark brown in colour when the chicks left the nest. The eyes could only be considered truly open and functional on day six or seven. The colour of the iris was brown, the same as in the juvenile yellow-billed oxpecker (Dowsett 1965).

Plate 16. Ten day old chicks of the red-billed oxpecker in the Satara area, December 1974.

Plate 17. A 19 d old chick of the red-billed oxpecker in the Satara area, December 1974.





Legs and claws

At hatching the legs were pink and the claws a very light grey colour. The legs and claws began to darken on day six and had a dark brown colour when the chicks left the nest. The mean growth rate of the tarsometatarsus calculated from measurements of 13 chicks and is given in Fig. 28. If the tarsometatarsus was measured from the depression in the angle of the intertarsul joint to the base of the complete scale before the toes diverge, the mean length of the tarsometatarsus in the adult bird was 22,4 mm (n = 248, SEM = 0,10). With a growth rate of 1,0 mm per day it was clear that adult length was attained 14 days after hatching.

Bill

At hatching the bill was yellow with a white egg-tooth on the tip of the upper mandible. On day four the egg tooth darkened and a black ridge appeared on the dorsal part of the upper mandible. On day 15 this black line was completed and ended in a dark patch around the nostrils. When the chicks left the nest only the lateral side of the upper mandible was not pigmentated. Pigmentation in the lower mandible was much retarded and the tip only began to darken from about day 17. If the fledgling was observed from a distance, the yellow sides of the upper mandible and the yellow lower mandible gave the impression of a yellow bill. This corresponded with the description given by McLachlan and Liversidge (1970).

The growth rate of the culmen is given in Fig. 29. The culmen was measured from the tip of the bill to its union with the base of the skull. The mean length of the culmen of the adult bird was calculated as 17,07 mm (n = 249, SEM = 0,06). With a mean culmen length of 16,5 mm on day 25 and a growth rate of 0,5 mm per day it is apparent that the culmen is nearly full grown when the chicks leave the nest. It is not known at what age the egg-tooth disappears.

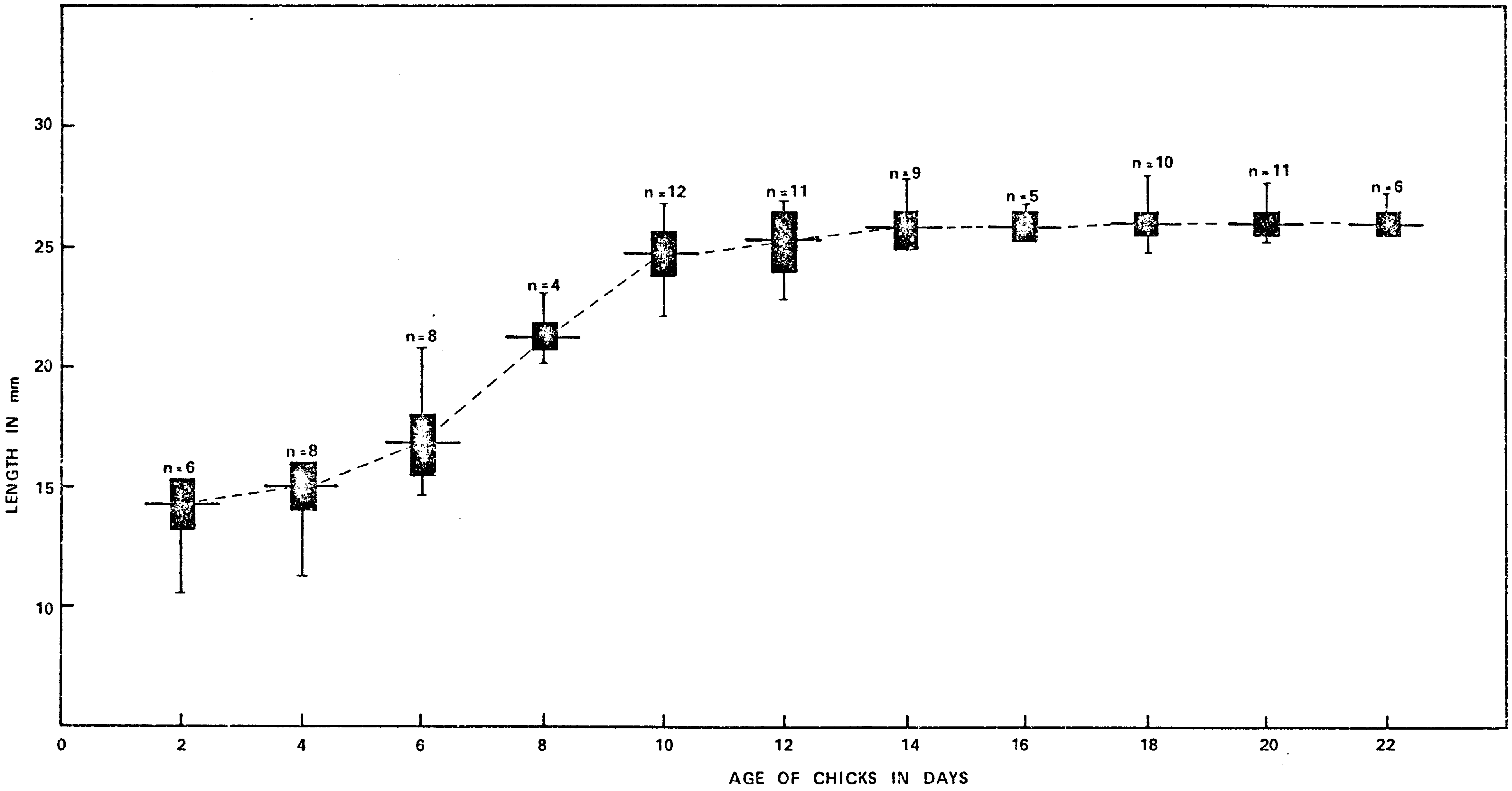


Fig. 28. The growth curve of the tarsometatarsus in 13 red-billed oxpecker chicks in the Satara area in the 1973/74 and 1974/75 breeding seasons. Vertical lines represent ranges, vertical rectangles show standard deviation and horisontal lines indicate the means

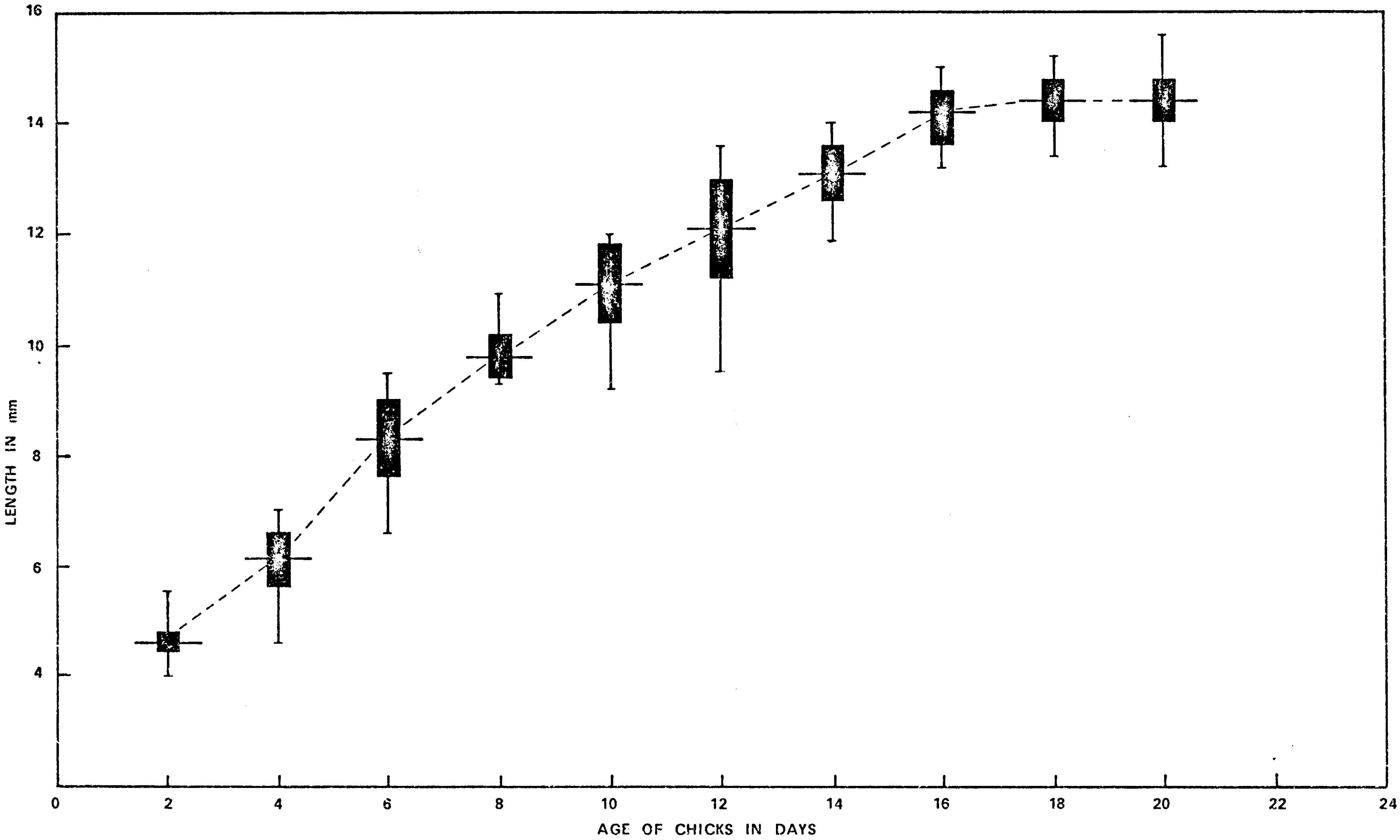


Fig. 29. The average growth curve of the culmen in 13 red-billed oxpecker chicks in the Satara area in the 1973/74 and 1974/75 breeding seasons. Vertical lines represent ranges, vertical rectangles show standard deviation and horisontal lines indicate the means

Body mass

The mass of the nestlings at hatching averaged 3,5 g (n = 3, SD = 0,74). In the oxpecker, the mass increase was relatively slow in the first two days, but became rapid and more or less constant up to day 11. The growth curve of the oxpecker is sigmoid in form, i.e. the slope of the growth curve (the absolute rate of growth) increased up to an inflection point (day 16) and decreased thereafter (Fig. 30). In the oxpecker it appears that the absolute rate of growth begins to decrease when the adult mass (49 g)(n = 250, SEM = 0,24) has been reached. On day 26 (the time the chicks started to leave the nest) the average mass of the chicks was 40 g which gives a mass decrease of 18%. Ricklefs (1968b) has found that peak nestling masses and subsequent mass recession in barn swallows (Hirundo rustica) were found to be due to the high water content of embryonic tissues, especially feathers, and the loss of water during the maturation of these tissues. According to Pettingill (1970) the mass of passerine birds increased again after fledging, though more slowly than before nest leaving, until by the time the young bird had attained independence its mass nearly equalled that of the adult female.

In the red-billed oxpecker, up to day 16, the average growth rate was 2,8 g per day. Mundy and Cook (in press) have found that the mass of the yellow-billed oxpecker increased at 4 g per day (n = 1) for 15 d and then decreased. Lack (1948) related the large clutches of hole-nesting species, as compared to open-nesting species, to their longer development periods, postulating that slower rates of growth resulted in decreased energy requirements of the young, thus permitting the parents to feed larger broods. However, Ricklefs (1968a) tested this hypothesis and found that hole-nesting and large clutches are not related through reduced growth rates. Lack (1948) also related the slow development of hole-nesting species to their relative freedom from predation and that the rate of development during any stage of the development period will bear an inverse relationship to the survival rate during that stage. Predation, however, appears to be high in oxpecker chicks in the Satara area (see section under survival of nestlings).

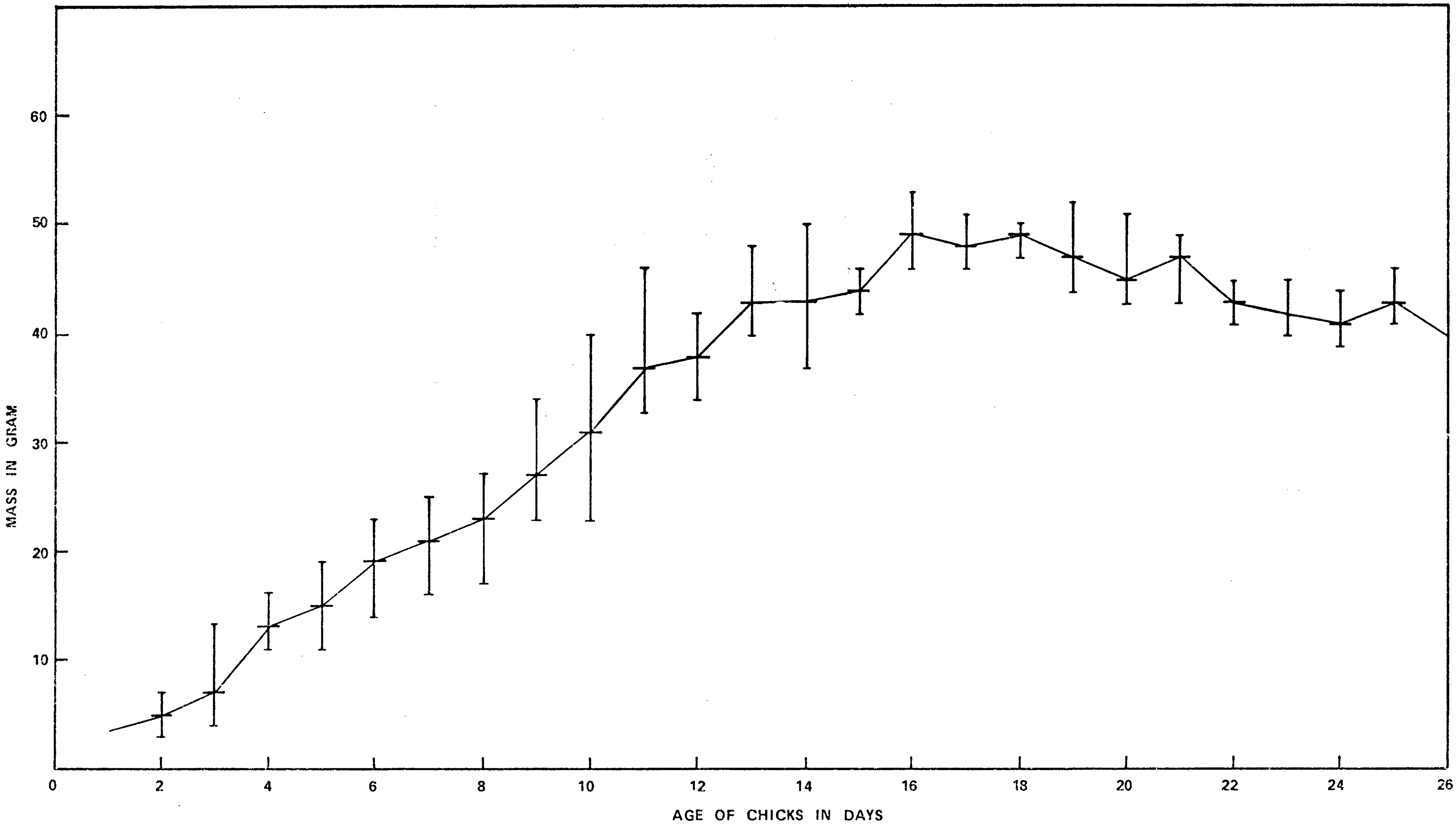


Fig. 30. Average growth curve of 13 red-billed oxpecker nestlings in the Satara area during the 1973/74 and 1974/75 breeding seasons. Vertical lines represent ranges and horisontal lines indicate the means.

The growth rate of the oxpecker nestlings in the same brood was mainly dependent on their relative ages which ranged from a few hours to three days. Figure 31, records the daily mass change of a brood of triplets, shows that the growth rates of first and second hatched chicks were almost identical, while last hatched chicks grew more slowly and their masses never approached those of the others. At day 10 the mass difference between the heaviest and lightest individuals was on the average eight grams, which indicates a mass difference of 29%. The smaller chicks also showed a greater mass loss, for a longer period, during adverse conditions. This can be seen in Fig. 31 on day 11 which followed two days of wet weather. Inclement weather may handicap the parent birds in their efforts to collect food for the nestlings. According to Ricklefs (1968a) differences in mass between siblings are often the result of competition for the food which the parents deliver. The development of feathers in these broods was not affected which indicated that the reduced growth rates reflected nutritional deficiencies rather than retarded development. However, Lack and Lack (1951) demonstrated how fluctuations in the availability of the food supply of the common swift (Apus apus) caused by inclement weather, retarded the growth of the young, not only in mass, but also in linear dimensions such as wing length. According to Lack (1954) deterioration of the food supply is often compensated for by a decrease in clutch size or by a reduction of the size of the brood by selective starvation in which case the growth patterns of the surviving young may be affected to a variable degree and he postulates that the number of young raised is limited by the parent's ability to gather food. Starvation was the cause of mortality in only one oxpecker nestling. This specific nestling was in a brood of four (the only brood of four found), fed by four adult birds. These chicks, however, were in a very small nest (maximum width of nest chamber was 9 cm), which could have resulted in an abnormally high competition for food as they grew older.

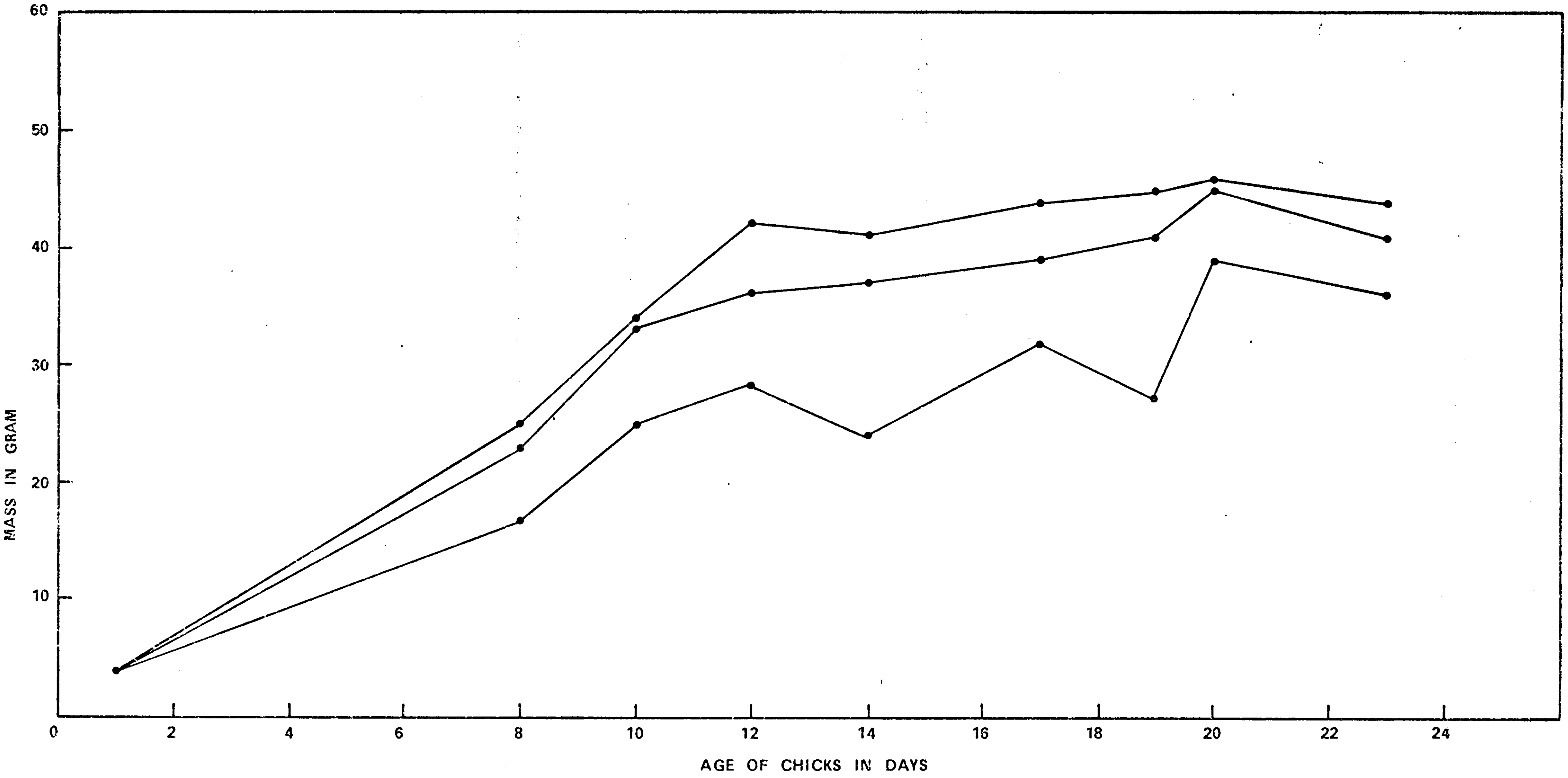


Fig. 31. Growth curve of three red-billed oxpecker nestlings of the same brood and fed by two adult birds in the Satara area in the 1973/74 breeding season.

The relationship between brood size and the average masses of nestlings is given in Table 41. These data was analysed statistically and a test on the coefficient of correlation showed that there is no significant relationship (t-test, $P > 0,05$) between brood size and the average mass of nestlings. The reason for this could be a bias originating from the small sample or because of poor feeding conditions occurring at different stages of growth in different young. Ricklefs (1968a) has found that as much as 30% variability may be present in both the asymptote and growth rate with respect to geographical locality, climatic conditions and season. Tarbotom (1971) has found in his study on the crimson-breasted shrike (Laniarius atrococcineus) that in one nest which was infested with mites (Ornithonyssus bursa), the growth of the nestlings was very much retarded compared with others. Oxpecker nestlings, however, infested with mites (Dermatophagoides sclerovestibulates) did not show any signs of retarded growth. The relationship between the number of adult birds in the group and the growth rate of the nestlings is shown in Table 41. These data were analysed statistically and no significant relationship (t-test, $P > 0,05$) was found. However, this could have been biased by the small sample ($n = 13$).

General development of behaviour

Data on some aspects of behavioural development are summarised in Fig. 32. On day one the chicks lay motionless at the bottom of the nest but responded by gaping when they were touched or when the nesting branch was moved. During gaping the chick raised its head and opened its bill while supporting its body with its wings. The inside of the mouth of a chick was bright orange with a yellow gape. As the chick grew, the gape swelling shrank. By the time the chicks left the nest, the gape swelling had all but disappeared and remained only as a thin yellow line until it disappeared altogether.

From Fig. 32 it is apparent that mobility developed gradually. Although a chick could crawl from day four, motor co-ordination was poor, especially for the legs. Only on day six did the

Table 41 : Average mass of chicks in different brood sizes on day ten compared with number of adult birds in a group of the red-billed oxpecker in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Number adult birds in group	Number of chicks in brood	Average mass of chicks on day 10 in g	Total number of chicks weighed
2	1	35	1
2	2	37	2
2	3	30	3
3	1	40	1
4	1	30	1
4	3	29	3
5	2	36	2
Total			13
Range		29-40	
SD		10,27	

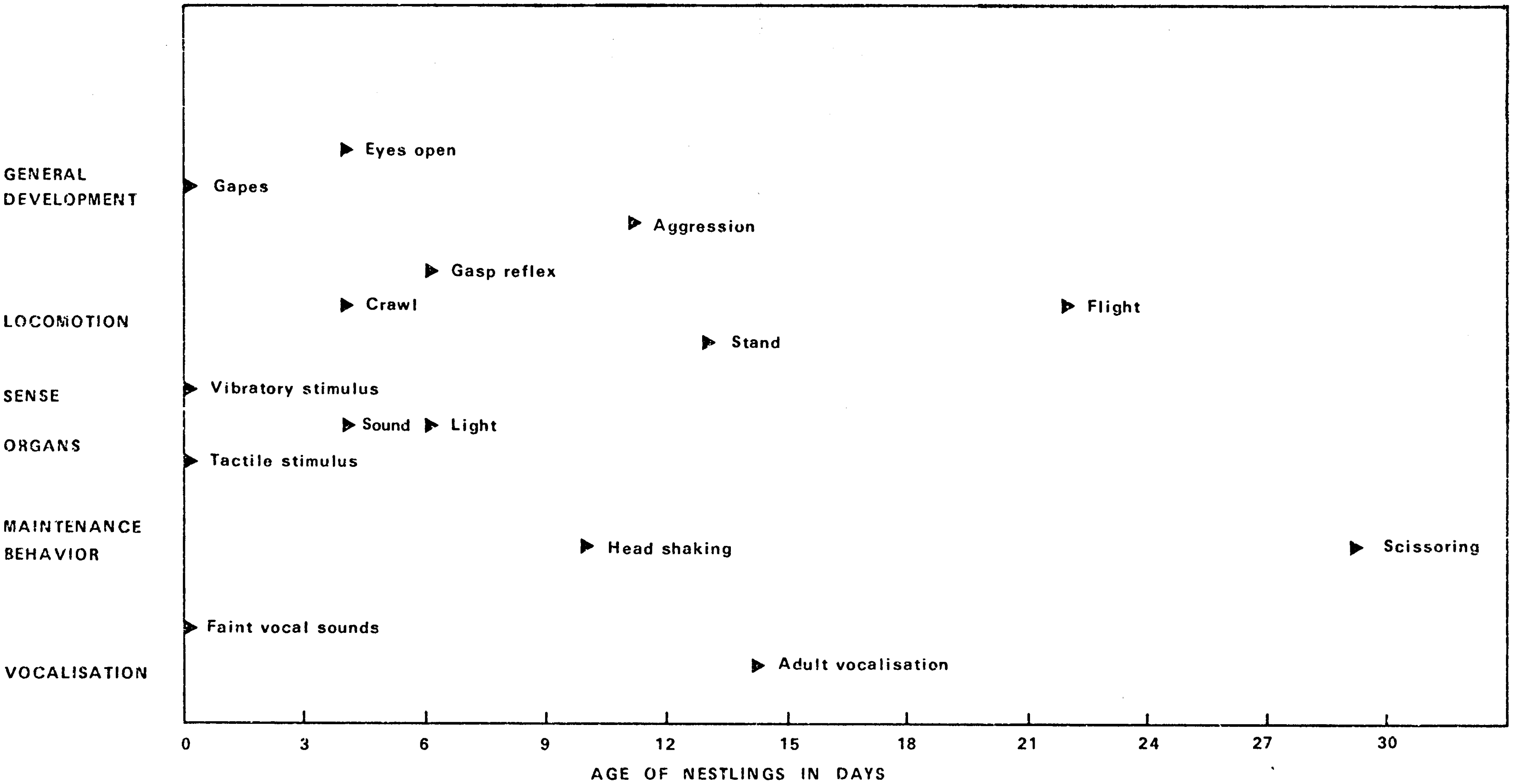


Fig. 32. Development of reflex responses and behaviour patterns in the red-billed oxpecker nestlings in the Satara area during the 1973/74 and 1974/75 breeding seasons

co-ordination between the wings and legs improve, and crawling became more vigorous as the grasping reflex developed. The chick could stand upright on day 13 without the support of the wings. A chick that jumped from the nest on day 22, was able to fly to a tree about 20 m away.

Before the eyes open and up to day 11, the chicks reaction to a hand inserted into the nest chamber was to beg with the bill vertically upwards. According to Von Haartman (1957) the gaping reaction of the hungry young in a number of hole-nesters is released by darkening of the nest. In the oxpecker, however, this gaping reaction was also released when a light was pushed into the nesting chamber. According to Pettingill (1970) the gaping reaction is released in the chick on receiving any vibratory or tactile stimulus from its parent, or from a like stimulus simulated by a person at the nest. As the nestling developed and its eyes began to open, it responded to visual stimuli and directed its gaping towards them. The begging action itself gradually modified, the nestling stood in the nest, vocalised strongly, fanned its wings, and stretched accurately towards the food source. From day 11 aggression developed and increased as the chicks grew older. The chicks' intruder-reaction was to crouch flat on the chamber floor, hiss loudly and peck at any strange object. If removed from the nest, the chick showed escape reaction.

Because of the hole-nesting behaviour of the oxpecker, it was difficult to observe the development of maintenance behaviour. Head-shaking was observed on day ten. A chick removed from the nest on day 15 displayed several maintenance activities, particularly preening and head-scratching. At the same time it displayed such comfort movements as stretching, yawning and shaking. When defaecating, the chick simply raised its posterior abdominal region, lifted the tail and voided the faecal matter: On the first day faint vocal sounds accompanied the gaping reaction. These vocal sounds can be described as a soft "tji-tji-tji" and a "chuur" if disturbed. Adult vocalisation, in the form of the contact call, was heard on day 14.

Behaviour of nestlings during the fledging stage

About two days before the nestlings left the nest, they were fed just outside. These nestlings reacted on the contact call of the parent birds and once outside the nest, they followed the parent birds around, begging for food. When begging the nestlings would vocalise strongly, fan the wings, and stretch towards the food source. These nestlings were also observed to perform scissoring movements against the nest branch. Wing exercise was observed in the form of wing-fanning. The adult birds removed any faecal sacs dropped by the nestlings outside the nest. The nestlings immediately returned to the nest after the adult birds flew away or if the alarm call was given.

On the day the chicks left the nest, the adult birds were observed to avoid the nestlings sitting outside although they brought food to the nest. Adult birds were observed to fly away from the nest with food, without feeding the chicks. According to Pettingill (1970) observers have sometimes credited parents with prompting their offspring to fledge by intentionally witholding food and thus enticing them to leave the nest. What seems to be an intent on the part of the parents is simply their hesitation, occasioned by some undetermined cause, in bringing the food (Lawrence 1967). Any such break in routine increases the young birds' hunger and their consequent aggressiveness. The following was observed when two oxpecker nestlings left the nest:

a. The nestling joined the parents when they gave the contact call and flew away from the nest.

b. The nestling flew into the air during a session of wing-fanning and joined the parents who flew away at the same moment.

According to Pettingill (1970) the young bird leaves the nest of its own accord on the maturing of an inherent impulse or instinct to do so. The action may be triggered by any one of a number of factors such as discomfort from high air temperature, hunger, exuberance during a session of wing-fanning, or a period of restlessness among the nest-mates, if they are the same age. Once the young oxpeckers fledges from the nest of its own accord, it does not return to the nest for roosting purposes. However, a nestling that jumped from the nest prematurely, due to the presence of the observer, returned to the nest for another two days. In two instances, the nestlings fledged between 06h00 and 09h00. The adult birds were observed to return to the nest the day after the nestlings left.

Nestling period

The age at which the chicks leave the nest varies within the species, and between the siblings of one brood. The trend is for the younger chicks to take longer to leave the nest compared with the older siblings. The overall average nestling period is 30 d (n = 4, SD = 2,24) but, even comparing the eldest chicks of different broods, there may be up to four days difference in age at leaving the nest. McLachlan and Liversidge (1970) give the nestling period of the red-billed oxpecker as 28 - 29 d. The nestling period is thus about twice as long as the incubation period which corresponds with the hypothesis of Von Haartman (1957) that hole-nesting birds have a relatively long nestling period.

The increased nestling period for the younger chicks appeared to be due to their greater response to times of food shortage, and slower recovery from such times. In all cases there was an age difference between the members of a brood due to their not being hatched simultaneously. At one nest the youngest chick fledged two days after the oldest chick.

According to Van Tyne and Berg (1959) opinion among ornithologists differs on how much human interference affects the length of the normal nestling period. Most of them agree that daily weighing or banding in the latter part of the nestling period does shorten that period and data obtained from such nests is not reliable. In the study on the oxpecker in the Satara area, it was found that at two nests where the nestlings were handled every second day, the mean nestling period was 26 d (n = 3, SD = 1,41). This is four days shorter than where the nestling period was observed without interference at the nest (30 d).

Predation of eggs and nestlings

Survival of eggs

From a total of 72 eggs in the 1973/74 and 1974/75 breeding seasons, the predation rate was calculated as 32%. Only one nest containing three eggs was deserted. No account can be given of the majority of eggs that disappeared. Broken eggs were found only beneath two nests. If predation and hatching success of the eggs are considered (see section under hatching success), it can be calculated that in the Satara area only 49% of all the eggs laid, hatched during the 1973/74 and 1974/75 breeding seasons. If the survival rate of the nestlings is also taken into consideration it appears that 40% of eggs laid, produced chicks that left the nests.

Survival of the nestlings and behaviour towards predators

During the 1973/74 and 1974/75 breeding seasons, in eighteen nests where 55 young hatched successfully only 45 (82%) left the nest. The survival rate in the 1973/74 breeding season was 86% and in the 1974/75 breeding season 82%. This gives a reproductive success of 0,8 fledglings per adult bird during the 1973/74 breeding season and a 0,5 fledglings per adult bird in the 1974/75 breeding season. However, only those nests in which birds were successful in hatching chicks were taken into consideration. The total reproductive success would thus be much lower. The factor of human interference must also be taken into consideration. According to Cumming and Steyn (1965) small predators such as mongooses, will follow a scent trail left by humans. With the result that these efforts to study the oxpecker may have contributed to the high mortality rate in the Satara area. In the literature, there are no data on the nesting success of oxpeckers from other areas to compare the data obtained in this study. Moreover, no data are available on the nesting success of passerine hole-nesting birds in the Kruger National Park. In a long term study by Flegg and Cox (1975) on a blue tit (*Parus caeruleus*) and great tit (*P. major*) colony at Kent, the lost rate due to predation were 38% and 36% respectively.

Royall (1966) found the egg-to-fledging success in a colony of starlings (*Sturnus vulgaris*) in Arizona to be 52,3%. Compared to these studies, the oxpeckers have a relatively low mortality rate in the Satara area.

Anti-predatory behaviour consists of a bird diving at a predator while giving the high intensity alarm call (for a description of the vocalisation of the oxpecker, see Stutterheim in prep.). This behaviour was shown towards a slender mongoose (*Herpestes sanguineus*), white-throated monitor (*Varanus exanthematicus*), bush squirrel (*Paraxerus cepapi*) and a red-and-black-billed kingfisher (*Halcyon senegalensis*). In all the cases observed, the oxpecker was successful in chasing the predator away from the nest. No anti-predatory behaviour was observed when a baboon (*Papio ursinus*) was sitting near the nest. Mobbing was only observed once when two adult birds joined a fork-tailed drongo (*Dicrurus lugwigii*) in mobbing a banded harrier-hawk (*Polyhoroides typus*) sitting in a tree about 30 m from a nest containing two chicks. Distraction displays were not observed in the oxpecker.

The majority of missing chicks disappeared unaccountably. Predation was observed only once when a Wahlberg's eagle (*Aquila wahlbergi*) caught a nestling sitting outside the nest. According to Steyn (1973) the Wahlberg's eagle shows a high preference for cathing young birds recently out of the nest. Attempted predation was observed when a ground hornbill (*Bucorvus leadbeateri*) tried to reach three chicks in a nest. At one nest the rotten remains of a chick was found which probably died of starvation (see section under body mass). Only at one nest were the partly eaten remains of a 22 d old chick found.

Table 42 shows the age of the oxpecker nestlings which disappeared from the nests in the 1973/74 and 1974/75 breeding seasons. A test on the coefficient of correlation showed no significant relationship (t-test, $P > 0,05$) between the mortality rate and age of the chicks. A significant

Table 42 : Predation of red-billed oxpecker nestlings of different ages and from different nests in the Satara area during the 1973/74 and 1974/75 breeding seasons.

Age of chicks in d	Number of chicks	Accumulated percentage from total number* of nestlings	Height of nests at which predation occurred in m
1	1	2	7
3	2	6	8
8	3	12	3
10	1	14	13
19	1	16	14
22	1	18	8
Total	9		
Range			3-14
Mean			8,8

* n = 55

relationship (t-test, P< 0,05), however, existed between the height of the nest and the survival of the chicks. In nests lower than ten meters, predation was as high as 29% compared to 4% predation in nests higher than ten meters (Table 42). The reason for this could be that low nests are more accessible for ground predators than high nests. The accessibility of the nesting chamber could also affect the mortality rate.

Brood size

From a total of 55 chicks (27 broods) the avergae brood size was calculated as 2,0 (SD = 4,35) for the 1973/74 and 1974/75 breeding seasons with an average brood size of 1,9 (18 broods) (SD = 3,74) for the 1973/74 breeding season and 2,2 (9 broods) (SD = 2,11) for the 1974/75 breeding season. According to Lack (1947) late broods tend to be larger than early broods. In the oxpecker the average size of the early broods was 1,9 (n = 18) compared to the avergae size of the late broods as 2,0 (n = 9). No correlation (t-test, P > 0,05) was found between the group size and the size of the brood (Table 43). This could be a bias from the small sample. Brown (1975), however, has found a positive and statistically significant correlation between the number of young fledged and the adult group size in the Arabian babbler (Turdoides squamiceps).

Renesting and the nesting season

According to Van Tyne and Berg (1959) the length of a breeding season can be defined as the number of months in a year during which one may find the nest of a particular species in a given locality. The data of commencement of nesting in the 1973/74 breeding season was calculated from the sighting of the first fledgling on 5 December 1973. In the oxpecker the average brood, from the day the first egg was laid until the last nestling had fledged, was 42 days. According to these data, the egg from which this specific chick had hatched must have been laid on about 24 October 1973. The last chick fledged on 14 April 1974. If the time needed for nest-building is taken as eight days, the length of the 1973/74 breeding season can be calculated as 184 days.

Table 43 : Group size in adult red-billed oxpeckers as correlated with brood and clutch size in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Group size	% occurrence	Average clutch size	Average brood size	Number of broods	Number of groups recorded
2	9	2,9	2,1	6	3
3	28	2,6	1,5	6	5
4	47	3,1	2,5	9	6
5	14	2,7	1,6	6	4

The red-billed oxpecker, being a multiple brooding species is successful in raising up to three broods in a season. In a total of 14 nests in the Satara area, eight groups bred once (58%), four groups bred twice (28%), and two groups bred three times in succession (14%). Renesting after the destruction of a nest with eggs or with young, is not referred to as multiple brooding. The average time elapsed between the fledging of one brood and the re-laying of the next clutch was calculated as 13 days - range, 10 to 16 days. This indicates that the oxpecker is capable of recycling very rapidly. These results were obtained from nests where the nestlings were colour marked and if these colour marked fledglings were observed at the same nest with the same number of adult birds, it was speculated that it was the same group that was breeding for the second or third time. Only at one nest were the adult birds colour marked. The interval between the destruction of eggs or young and the first eggs of the next set was calculated as 31 to 51 days (average, 41 days). According to Willis (1967) repeated nesting throughout the breeding season is likely to be characteristic of birds exposed to high losses of nests from predation. This corresponds with the high predation rate observed in the Satara area.

Post-feldging period

When leaving the nest, the fledglings are taken directly to the mammalian symbionts. They do not return to the nest for roosting purposes, and must therefore be roosting with the adults elsewhere. After fledging, the young utter the begging call when sighting an adult and will even beg for food from approaching fledglings. When begging, the fledgling would vocalise strongly, fan its wings and stretch towards the food source. It was not possible to establish accurately at what age the young started to feed for themselves. Juvenile birds, however, were observed to be fed until about 90 days of age. From these observations it seems that the fledglings remain at least partly dependant on the parents for perhaps two months after leaving the nest.

When renesting, the fledglings were observed to accompany the adults to the nest. At one nest, during the incubation period, the nestlings joined the adult birds in 20% of the visits. However, at the same nest during the nestling period, the fledglings were observed to accompany the parents in 57% of the visits. It can be speculated that the food brought to the nest by the parent attracted the fledglings. At one nest, containing three chicks of a later brood, a fledgling, 63 days old, was observed to enter the nest and remove a faecal sac. At the same nest, a fledgling of the first brood, was observed to accompany a fledgling of the second brood, in the absence of any adult birds. It is doubtful, however, if the elder fledgling was feeding the younger fledgling. The survival value could be that the fledgling from the later brood may benefit from learning where food is to be found and also through acquiring an increased awareness of the approach of predators. The same fledgling at an age of 76 days, was observed to put his bill into the open mouth of a begging nestling of the next brood which was sitting outside the nest. It could not be ascertained whether that fledgling was feeding the chick. Fledglings of the first brood were sometimes also observed to enter a nest containing chicks of later broods. This behaviour was also observed at nests containing eggs. Because of the hole-nesting behaviour of the oxpecker, it was impossible to see whether they were actually feeding the chicks. Chicks in captivity were observed to imitate the feeding action although they were not actually feeding each other. There was thus no positive proof that fledglings of one brood actually assisted in providing food for the later broods. Fledglings were also observed to accompany the adult birds when chasing predators from the nest. The actual role of the fledgling in the anti-predator behaviour is not known but it can be speculated that they only followed the adult birds.

In the literature various colour descriptions of the bill of the juvenile oxpecker are found: dull red with a black tip (Van Someren 1951), all-yellow (Winterbottom 1952

In: Mundy and Cook (in press), dusky-brown or blackish (Pitman 1956 and McLachlan and Liversidge 1970), dark bills (Attwell 1966). The colour change of the bill in two chicks of known age, raised in captivity was from yellow to black followed by a gradual change to the red adult coloration. The duration of colour change in these chicks was, however, delayed if compared with that of free-flying fledglings. In the wild, it was not possible to establish accurately at what age the young started to acquire the next colour phase, as it was a gradual change. When the chicks leave the nest, the bill is yellow except for a dark pigmentation on the dorsal part of the upper mandible and tip of the lower mandible. At about day 60 this dark pigmentation is completed and the bill appears black or dusky-brown. From about day 120 a red coloration appears on the proximal side of the upper and lower mandible. When about seven months old, the bill has attained the adult coloration except for a black strip on the dorsal part of the upper mandible and a black patch around the nostrils. This dark pigmentation disappears within the next month.

When the chicks left the nest the colour of the iris was brown. When about four months old, a yellow ring appeared on the inner side of the iris. This yellow coloration progressed outwards and the adult coloration was attained at about the age of six or seven months. When the chicks left the nest, the colour of their plumage appeared to be of a much darker grey than the normal adult coloration. The juvenile birds underwent a partial post-juvenal feather replacement at about three months of age. In this cycle all the feathers were replaced except the primaries, secondaries, rectrices and primary coverts. This partial post-juvenal feather replacement was completed at about the age of six months. After this feather replacement the coloration of the plumage was about the same as that of the adult birds.

A total of 15 chicks were colour ringed during the 1973/74 breeding season. Resightings of those birds during the 1974/75 breeding season indicated that they returned or stayed in the breeding area. The maximum distance of a bird sighted at a nest was about one kilometer from the ringing locality or nest used during the 1973/74 breeding season. That specific bird was also resighted during the winter months, at a water hole 500 m from the ringing locality. The nest at which that chick was ringed, was used by a Burchell's glossy starling (Lamprotornis australis) during the 1974/75 breeding season. Oxpeckers started to use the nest at the stage of nest building at the beginning of the breeding season but it was taken over by the starlings.

Home range and territorial behaviour in breeding birds

According to Von Haartman (1958) competition for nest holes instead of food has caused the evolution of localised territoriality is hole-nesters and the development of territorial behaviour only after finding a suitable hole. Intraspecific aggression at a nest was only observed once when an adult bird approaching a chick sitting outside, was chased from the nest by two other adult birds. Aggression was without physical contact in a brief aerial chase. The role of the sexes in nest defence is not known.

Resightings of adult birds which were colour marked at a nest, were used to determine the size of the home range during the breeding season. That specific nest was located on the banks of the Nwanedzi river about 6 km south of the Satara rest camp. From a total of 11 resightings of that group, a circular activity zone of 7,0 km^2 was calculated from a maximum observation distance of 1,5 km from the nest. The Satara area supports a game population of 7,500 kg/km^2 of mixed mammalian species (Pienaar 1966). Hence in whatever direction a bird or a group of birds may fly, they will soon encounter sufficient quantities of suitable food provided by the ungulate concentration. This could be the reason for the small activity zone observed in the breeding group. However, as the oxpecker feeds on mobile species, it can be speculated that the home range has indefinite boundaries which are determined by the distribution of the mammalian symbionts on any given day.

At night, only one bird, the active female, stayed with the eggs or chicks in the nest. As no permanent roost was found in the Satara area, no account can be given of the distance travelled between the roosting area and the nest locality. The only two permanent roosting areas found in the Kruger National Park were located in ilala palms (Hyphaene orinita) (see section under roosting behaviour). The nearest ilala palms from the nesting site occurred along the Sweni river, about 10 km away. If the ilala palms along the Sweni river were used as a roosting area, the activity zone was highly underestimated. No evidence was, however, available to support this postulation.

Population dynamics

From the breeding data, the replacement rate of oxpeckers during the 1973/74 breeding season was calculated as 0,8 chicks per adult. From a count made in the Satara area during 1973 (at the end of the breeding season in April), the reproductive success was calculated as 0,72 juveniles per adult from a total of 139 birds. Another count made during July 1974 gave a reproductive success of 0,64 juveniles per adult from a total of 74 birds. This indicates a mortality rate of 12% for juvenile birds over a period of three months. The replacement rate during the 1974/75 breeding season was calculated from the breeding data as 0,5 chicks per adult. From a count made during July 1975 in the Satara area the reproductive success was calculated as 0,34 juveniles per adult from a total of 171 birds. This indicates a mortality rate of 32% for juvenile birds over a two month period.

Discussion

In the absence of a bigger sample of marked birds, a lengthy speculation on the significance of various phenomena observed in the social organisation and breeding biology of the red-billed oxpecker is not warranted, but some discussion will serve to identify the principal issues, some of which could be resolved by suitable further manipulation in the field.

According to Lack (1968) the term co-operative breeding is normally restricted to those species in which more than one pair share in building a nest, laying the clutch or helping to feed one brood. Skutch (1961) reviewed the phenomena of co-operative breeding and in about 50 species in nearly all instances such helpers are males. Within the Buphaginae the evidence suggests a correlation of the occurrence in multiple breeding units. In the red-billed oxpecker the breeding unit consists of two to five birds. All the birds in the group help to search for the nest, build the nest and feed the young. As it was impossible to determine whether the group had only one nest, it can only be speculated whether the helpers were unmated helpers or mutual helpers.

In the Skukuza area the sex ratio of the oxpecker is 1,01 (129 specimens). The co-operative breeding can thus not be explained in terms of surplus males as is the case in the pied kingfisher (Ceryle rudis) (Douthwaite 1970; In: Fry 1972). In the oxpecker the helpers are of both sexes and comprise 45% of the breeding population which has a balanced sex ratio. The same was found in the kookaburra (Dacela gigas)(Parry 1968, In: Fry 1972). Since D. gigas are sexually mature at one year, their system of helpers at the nest, with its dominance hierarchy based on age, sex, and breeding experience is thought to be a long-term population regulatory device.

The adaptive significance of communal nesting is not clear. Lack (1968) reviewed communal nesting and evidence available to him, showed that pairs with "helpers" raise more young than unaided pairs. He could thus explain the evolution of the system in terms of natural selection. The Darwinian theory, as modified and developed by Lack (1968), holds that natural selection favours those individuals that contribute the greatest number of individuals of the next generation. Reproductive rates of any species or population will therefore tend to represent the maximum effort possible under the average prevailing conditions. In addition, the supernumerary birds thereby assist the survival of close relatives with the same genes. Zahavi (1974) has found that the Arabian babbler (Turdoides squamiceps) defend territories during the breeding season and it is thus reasonable to assume that at least part of the regulation of the population is controlled within each group. Competition should therefore exist among adult birds on the limited chance to reproduce in the sole nest in the territory and competition can also be expected between fledglings and older non-breeding birds within each group. It is therefore apparently paradoxical to find that birds "help" at the nest. The critical question is to determine if these birds are really helping. In the oxpecker, competition for food was frequently observed between nestlings and fledglings. Rowley (1965) has found that in the superb blue wren (Malurus cyaneus) fewer birds survived among fledglings which were cared for by helpers than among fledglings which were tended only by their parents. However, in M. cyaneus large groups produced more offspring than single pairs. In addition, M. cyaneus helpers take charge of the fledglings when they leave the nest, thus enabling the pair to start a second brood more quickly than single pairs, which have to feed their brood after they have left the nest. Fry (1972) has found in the red-throated bee-eater (Merops bulocki) that on the average more young were reared by multiple units than by pairs, but production of fledged young per adult was less for pairs with helpers than for unassisted pairs. However, these differences were not statistically significient. Fisher (1958, In: Brown 1975) speculates that the presence of helpers with their parents raises the fitness of the parents over that of parents without helpers by promoting the survival and maturation of the helpers. In this view the helpers do not contribute significantly to the raising of more young and they may even slightly hinder reproduction and/or survival of others in the group. In addition, non-breeding birds, by staying in the vicinity of the nest, may reduce the food available for the nestlings and consequently lower the reproductive success of the breeders. The activity of the group, around a nest or around a fledgling, may increase the chances of a predator finding the young birds (Koster 1971, In: Zahavi 1974). Parents would therefore tolerate such young only because they constitute the progeny with the highest reproductive value.

In the oxpecker, groups of two are rare (9%). Since it is precisely in these groups that the lack of helpers should contrast most with typical groups of four and five, the most critical test of correlation of fitness parameters with group size could not be made. This could be the principal reason for the lack of correlation in the data. However, according to Brown (1975) the rarity of groups of two in nature suggests that they are significantly less fit than groups of four and five. In addition, he also speculates that there may exist, in theory at least, an optimal group size and it is reasonable to suggest that the commonest group sizes in nature are the optimal ones. With this assumption the mathematical function describing the relationship between group size and fitness, should have the shape of an inverted U, with both large and small group sizes being selected against. With such a function one would not expect to find a significantly positive correlation between group size and fitness. In the oxpecker the commonest group size is four (47%). From Table 43 there is a suggestion of such a function with the four-member group the most successful. However, the three-member group does not fit in with this speculation.

The age at which the oxpecker can reproduce is not known. According to Rowley (1965) in M. cyaneus, males stay with their parents for up to three years but may breed successfully on their own when a year old. However, in M. cyaneus there is a surplus of males in the population because females disperse after fledging and may became exposed to predation or food shortage. Since in the oxpecker the extra helpers are of both sexes, this implies that it is difficult for young inexperienced pairs to raise young on their own. In addition, young birds which defer their breeding maturity must have gained considerable experience of provisioning and other nesting duties if they had helped in previous years at the nest of a breeding pair, and this would enhance their survival and success at their own first breeding attempt. Furthermore, if one adopts the hypothesis that the population is self-regulated below the limit imposed by food resources (Wynne-Edwards 1962), then it is tenable that the substantial non-breeding community provides a reserve of experienced birds for recruitment into the breeding population to compensate its annual loss.

According to Dowsett (1965) the extra helpers in the Buphaginae enabled the necessary food to be obtained at a difficult time of the year. He speculates that for the oxpecker it must be considerably more difficult to find their hosts during the rains than in the dry season, because the mammals are considerably dispersed and symbionts difficult to see in thick vegetation in the wet season. No evidence is, however, given to support this speculation. From Table 41 it is clear that no correlation exists (t-test, $P > 0{,}05$) between the number of birds in the breeding unit and the growth rate of the chicks. Furthermore, with only one chick observed to die of starvation in both breeding seasons, it appears that food was not a limiting factor in the Buphaginae during the two breeding seasons in the Satara area. It can thus also be speculated that no correlation exists between food and the size of the breeding group. The agonistic behaviour observed on the mammalian symbionts could, however, point to the fact that food could be a limiting factor, at least during certain times of the year.

CHAPTER 9

ECTOPARASITES

Introduction

Arthropod ectoparasites are still imperfectly known. In the literature, no reference was found to any ectoparasites on oxpeckers. A better knowledge of the occurrence and host specificity of ectoparasites, may shed light on the cause and transmission of disease, delineate relationships of various groups of birds, and provide a better insight into different aspects of zoogeography (Watson and Amerson 1967).

Results

Ectoparasites of adult birds

Mites

Pterodectes buphagi (Till). This species inhabits the wing and tail feathers along the shafts of which the eggs are laid. This feather mite was found in very high numbers on most of the specimens examined.

Ticks

Amblyomma hebraeum (Kock, 1844). This species was only found on the head region and around the anus. No adult specimens were found on the oxpecker. According to du Toit and Theiler (1964) this is a three-host species of which the immatures are often found on small mammals and birds. It is interesting to note that A. hebraeum is a common prey species of the oxpecker. However, ticks can be described as rare in adult oxpeckers. A. hebraeum is probably picked up when feeding on the mammalian symbionts.

Lice

Sturnidoecus sp. n. According to Ledger* (pers. comm.) this is probably a new species and the description must wait for the revision of the genus. This feather louse was very common on the head region, breast and back of adult birds.

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Louse flies

Hippoboscid flies were observed twice on adult birds but these flew away before they could be collected.

Ectoparasites of nestling birds

Skin mites

Dermatophagoides sclerovestibulatus (Fain, 1975). This was a new species described by Fain (1975). It was found in high numbers on nestlings at two nests in the Satara area. These mites were found to move all over the body close to the skin and did not appear to be restricted to any particular region.

Ticks

Amblyomma hebraeum (Kock, 1844). Commonly found on the nestlings and not restricted to any particular region. As it is quite dark in the nests and ticks are not digested before being fed to the chicks, these ticks could have escaped during the feeding process (Stutterheim in prep.).

Boophilus decoloratus (Kock, 1844). Only five specimens were found on the nestlings in the Satara area. *Boophilus* was not restricted to any particular region and was found on the rump, abdomen, head region and around the anus. As they were found only on the nestlings, these ticks perhaps escaped during feeding. However, Theiler (1962) gives four records of adult *B. decoloratus* found on birds.

Discussion

Preening is considered to be important in keeping ectoparasites in check in birds (Boyd 1951). Although 11% of the duirnal time budget of the red-billed oxpecker is devoted to preening, it would appear that oxpeckers harbour a large population of ectoparasites. However, Ash (1960) and Ledger (1970) have pointed out that preening is probably only one of several factors in controlling ectoparasites in wild birds; moreover, distribution of ectoparasites on the host, seasonal patterns in abundance and reproduction of the ectoparasites and the ecology of the birds could also play an important role in infestation. The occurrence of *A. hebraeum* and *B. decoloratus* is a unique example of prey species parasitising its predator. No zoological term exists to describe this relationship.

SUMMARY

The red-billed oxpecker (B. erythrorhynchus) is highly adapted for a complicated and intimate relationship with certain large mammals. Progression on the mammals is either by hopping, walking or climbing. The flight is direct but undulating which appears to be a flap followed by a glide. Four feeding methods are used e.g. scissoring, plucking, pecking and insect cathing. The mammalian species utilised play an important part in their drinking behaviour because animals present at a water point are used as a platform from which the bird flies down to the water and back after drinking. Although the food preferences of the oxpecker indicate a high water content it appears that they do not have effective physiological mechanisms for water conservation. Three types of preening were distinguished: oiling, rubbing and wet-preening.

The feeding activity shows a morning and late afternoon peak and the duirnal time budget for feeding was calculated as 68%. Every peak in feeding activity is followed by a peak in resting with a maximum resting period between 11h00 and 13h00. Comfort movements are not dependant on a particular time of day. At high ambient temperatures the oxpecker prefers animals in the shade and at low ambient temperatures, animals in the sun.

The results obtained from marked birds at Skukuza show that the study population has no seasonal fluctuations in numbers and have little or no local movements. The maximum distance the oxpecker was observed away from the ringing locality measured 8,0 km with a mean distance of 3,37 km. For two birds, circular home ranges of 26 km^2 and 27,0 km^2 was calculated. Individual birds or groups, tend to feed in certain areas.

The primaries have a sharply defined moulting season, which extends mainly over an 11 month period. The mean time to replace a primary feather is 34 days. The moult of the secondaries is initiated at two points, at the first secondary

and at the innermost secondary. The secondary moult extends over a seven month period. The tertials moult in the normal middle/inner/outer passeriform fashion. The rectrices moulted only once annually. The two body moult cycles correspond with the moult of the tertials. First-year birds undergo a partial postjuvenal feather replacement at three months of age.

Searching for suitable nest holes is always done from the mammalian symbionts. Oxpeckers prefer to breed in C. imberbe trees in the Satara area. Animal hair, dung, grass and rootlets are the only material used for nest building. The average clutch size was 2,8. Eggs are laid before 09h00. The mean number of change-overs of incubating birds were calculated as 1,0 per hour and the feeding rate as 3,1 feeds per hour. The nest was kept clean throughout the chicks nestling period. Up to five birds regularly attend a given nest. All the members of a group feed the nestlings, guard them and later care for the fledglings. Only one female and one male participate in incubation. The growth curve of the nestlings are sigmoid in form and increase up to an inflection point on day 16 and decrease thereafter. Starvation was the cause of mortality in only one nestling. The overall average nestling period is 30 days. The reproductive success was 0,8 fledglings per adult bird during the 1973/74 breeding season and 0,5 fledglings per adult bird in the 1974/75 breeding season. A direct relationship existed between the height of a nest and the survival of the chicks. The length of the 1973/74 breeding season was calculated as 184 days. Juvenile birds are fed untill about 90 days of age.

Mites, ticks, lice and louse flies were found to be the ectoparasites of the red-billed oxpecker in the Kruger National Park.

SAMEVATTING

Die rooibek renostervoël is aangepas vir 'n ingewikkelde en intieme verwantskap met sekere groot soogdiere. Die voëls beweeg op die soogdiere deur te spring, loop of om te klim. Die vlug van die voëls is reguit maar wuiwend. Vier metodes van vreet is waargeneem nl. om deur die hare van die soogdiere te kam, voorwerpe af te pik of te pluk en om insekte te vang. Soogdiere wat deur die renostervoëls benut word, speel 'n belangrike rol in die waterdrink gewoontes van die voëls omdat soogdiere by water as 'n platvorm benut word om na die water en terug te vlieg. Alhoewel die voedsel van die renostervoël 'n hoë konsentrasie water bevat, bleik dit dat die voëls nie 'n effektiewe fisiologiese water-besparings meganisme besit nie.

Die vreet-gewoontes van die renostervoëls beslaan 68% van die totale aktiwiteit gedurende die dag en toon 'n oggend en laat middag piek periode. Die voëls rus maksimaal tussen 11h00 en 13h00 en elke piek periode van vreet word gevolg deur 'n periode van rus. By hoë omgewings temperature verkies renostervoëls soogdiere wat in die skaduwee staan terwyl by lae temperature soogdiere wat in die son staan, verkies word.

Deur 'n populasie voëls by Skukuza te merk is bepaal dat die voëls se bewegings beperk is en dat min of geen seisoenale fluktuasies in getalle voorkom nie. Die maksimum afstand wat die renostervoëls beweeg het, was 8,0 km met 'n gemiddelde afstand van 3,37 km. Die oppervlakte van die gebiede waar twee voëls aktief was, is onderskeidelik bepaal as 26 km^2 en 27 km^2. Daar is ook gevind dat sekere voëls of groepe voëls geneig is om in sekere spesifieke gebiede te vreet.

Die primêre vlerkvere van die renostervoëls besit 'n afgebakende ververings-seisoen wat strek oor 'n periode van 11 maande. Daar is bepaal dat gemiddeld 34 dae nodig is om 'n primêre vlerkveer te vervang. Ververiing van sekondêre vlerkvere begin by die eerste en by die middelste sekondêre vlerkvere. Die sekondêre vlerkvere verveer oor 'n tydperk van sewe maande. Die tersiêre vlerkvere verveer in die

normale middelste/binneste/buitenste volgorde. Stertvere verveer slegs een keer per jaar. Die liggaamsvere verveer twee keer per jaar en elke ververing-tydperk stem ooreen met dié van die tersiêre vlerkvere. Voëls wat jonger is as 'n jaar, ondergaan 'n gedeeltelike ververing op 'n ouderdom van drie maande.

Die soektog na geskikte nesgate vind vanaf die soogdiere plaas. Renostervoëls verkies om in die Satara omgewing in hardekoolbome te broei. Hare, mis, grasstingels en wortels was die enigste materiaal wat vir nesbou gebruik is. Renostervoëls lê gemiddeld 2,8 eiers op 'n slag. Eiers word voor 09h00 gelê. Voëls wat broei word gemiddeld 1,0 keer per uur afgelos en die kleintjies word gemiddeld 3,1 keer per uur gevoer. As die voëls broei word die nes skoongehou. Tot vyf volwasse voëls is by die neste opgemerk en al die voëls in die groep voer en beskerm die kuikens. Slegs een wyfie en een mannetjie broei op die eiers. Die groei-kurwe van die kleintjies is segmoïed in vorm en styg tot by 'n infleksie punt op dag 16 waarna dit weer daal. Slegs een kuiken het aan ondervoeding gevrek. Die gemiddelde tydperk wat die kuikens in die nes bly, is bepaal as 30 dae. Gedurende die 1973/74 broei-seisoen was die voortplantings sukses 0,8 kuikens per volwasse voël in vergelyking met 0,5 kuikens per volwasse voël in die 1974/75 broei-seisoen. 'n Direkte verwantskap bestaan tussen die oorlewing van die kuikens en die hoogte van die nes. Die lengte van die 1973/74 broei-seisoen is bepaal as 184 dae. Jong voëls word gevoer tot op 'n ouderdom van ongeveer 90 dae.

'n Groot aantal ektoparasiete in die vorm van myte, bosluise, luise en luis-vlieë is op die renostervoël in die Nasionale Krugerwildtuin gevind.

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Appendix 1 : Montly captures of the red-billed oxpecker at the animal pens of the Veteninary Division at Skukuza in the period March 1973 - December 1974.

				Accumulated						
Date	Ringed	Recaptures	Total caught	Ringed	Recaptures	Total	Per cent of accumulated new rings to totals	Per cent of accumulated recaptures to totals	Netting hours	Trapping success per ten hour trapping time
30/3/73	2	0	2	2	0	2	100	0	4	5
31/3/73	24	0	24	26	0	26	100	0	10	18
8/5/73	9	3	12	35	3	38	92	8	10	12
28/5/73	9	1	10	44	4	48	91	8	10	11
27/6/73	7	3	10	51	7	58	88	12	10	10
29/6/73	6	2	8	57	9	66	83	14	14	12
8/8/73	11	1	12	68	10	78	87	13	10	12
14/7/73	2	2	4	70	12	82	85	15	10	4
12/10/73	7	0	7	77	12	89	87	13	10	7
18/11/73	9	1	10	86	13	99	87	13	10	10
7/1/74	3	2	5	89	15	104	86	14	10	5
29/1/74	8	1	9	97	16	113	86	14	10	7
20/2/74	17	3	20	114	19	133	86	14	10	20
8/8/74	2	1	3	116	20	136	85	14	2	3
21/3/74	3	1	4	119	21	140	85	15	10	6
19/4/74	3	5	8	122	26	148	82	18	10	8
22/5/74	3	2	5	125	28	153	82	18	10	5
17/6/74	4	1	5	129	29	158	82	18	10	5
12/7/74	2	1	3	131	30	161	81	19	10	3
20/8/74	1	2	3	132	32	164	80	20	10	3
23/9/74	12	4	16	144	36	180	80	20	10	16
17/10/74	6	3	9	150	39	189	79	21	10	9
10/12/74	0	2	2	150	41	191	79	21	10	2
13/12/74	0	1	1	150	42	192	78	22	10	1
14/12/74	2	4	6	152	46	198	77	23	10	6
15/12/74	1	0	1	153	46	199	77	23	10	1
16/12/74	2	2	4	155	48	203	76	24	10	4
Totals	155	48	203						250	
Range	0-24	0-5	1-24						2-14	1-20

Appendix 2 : Frequency of captures of the red-billed oxpecker at the animal pens of the Veterinary Division at Skukuza in the period March 1973 - December 1974.

Number of times caught	Number of birds	Per cent of total
1	23	65,7
2	9	25,7
3	2	5,7
4	0	0
5	1	2,9
Total	35	

Appendix 3 : Dimensions of 43 red-billed oxpecker nests examined in the Kruger National Park in the 1973/74 and 1974/75 breeding seasons

Nest number	Tree Species	Height of nest entrance from ground (m)	Maximum width of nest chamber (cm)	Depth of nest floor below lip of entrance (cm)	Height of entrance hole (cm)	Width of entrance hole at widest point (cm)	Circumference of nesting branch (cm)	Direction nest entrance is facing	Colour nesting material	Height of nesting tree
1	Combretum imberbe	7	14	28	12	13	74	Vertical	Rufous	13
2	Combretum imberbe	9	14	21	12	4	131	SW	Rufous	14
3	Combretum imberbe	8	14	29	4	5	124	Vertical	Rufous	20
4	Combretum imberbe	9	9	29	16	5	72	N	Rufous	15
5	Combretum imberbe	7	10	28	6	6	62	NE	Rufous	13
6	Combretum imberbe	15	15	27	6	5	74	S	Rufous	18
7	Combretum imberbe	8	10	53	11	10	71	Vertical	Rufous	12
8	Combretum imberbe	6	12	54	11	10	62	Vertical	Rufous	15
9	Combretum imberbe	10	11	25	8	9	96	Vertical	Rufous	21
10	Acacia nigrescens	6	11	46	7	7	1002	Vertical	Rufous	6
11	Combretum imberbe	10	16	21	8	4	71	S	Rufous	16
12	Combretum imberbe	7	11	64	13	4	63	S	Rufous	11
13	Combretum imberbe	8	10	55	4	11	71	SW	Rufous	13
14	Combretum imberbe	13	17	20	9	4	99	N	Rufous	21
15	Combretum imberbe	6	12	18	4	9	62	N	Rufous	13
16	Combretum imberbe	8	10	27	7	8	92	NW	Rufous	12
17	Combretum imberbe	7	10	30	20	13	70	SE	Rufous	10
18	Spirotachys africanus	8	15	22	5	10	149	NE	Rufous	19
19	Combretum imberbe	14	-	-	-	-	-	N	-	23
20	Combretum imberbe	6	10	69	6	5	55	NE	Rufous	11
21	Combretum imberbe	7	13	48	16	6	103	Vertical	Rufous	8
22	Combretum imberbe	10	11	54	7	11	98	NE	Rufous	15
23	Combretum imberbe	7	12	47	3,5	5	69	NE	Rufous	13
24	Combretum imberbe	10	14	33	7	5	84	N	Rufous	15

Continue/.......

Appendix 3 continued

Nest number	Tree species	Height of nest entrance from ground (m)	Maximum width of nest chamber (cm)	Depth of nest floor below lip of entrance (cm)	Height of entrance hole (cm)	Width of entrance hole at widest point (cm)	Circumference of nesting branch (cm)	Direction nest entrance is facing	Colour nesting material	Height of nesting tree
25	*Combretum imberbe*	8	12	38	5	6	78	Vertical	Rufous	15
26	*Combretum imberbe*	10	12	39	7	6	74	N	Rufous	15
27	*Acacia nigrescens*	7	18	81	10	11	86	Vertical	Rufous	8
28	*Kigelia pinnata*	13	-	48	7	8	48	S	Grey	15
29	*Colophospernum mopane*	8	13	28	9	7	84	W	Rufous	14
30	*Combretum imberbe*	7	17	45	7	5	67	Vertical	Rufous	8
31	*Combretum imberbe*	8	17	65	7	15	59	E	Rufous	13
32	*Combretum imberbe*	7	12	50	6	17	124	W	Rufous	16
33	*Combretum imberbe*	6	12	44	4	9	77	W	Rufous	12
34	*Combretum imberbe*	7	17	23	6	4	86	SE	Rufous	12
35	*Combretum imberbe*	9	16	23	6	10	60	Vertical	Rufous	12
36	*Acacia nigrescens*	3	11	17	8	4	81	N	Rufous	7
37	*Combretum imberbe*	12	10	38	12	11	69	E	Rufous	14
38	*Combretum imberbe*	11	13	28	12	4	64	W	Rufous	13
39	*Combretum imberbe*	11	12	25	6	6	48	Vertical	Rufous	16
40	*Combretum imberbe*	8	15	33	7	5	81	S	Rufous	18
41	*Combretum imberbe*	8	11	30	11	6	90	NW	Rufous	12
42	*Combretum imberbe*	7	13	33	15	5	173	Vertical	Rufous	16
43	*Acacia nigrescens*	1,2	12	34	5	5	58	W	Rufous	2
	Mean dimensions	8,1	14,3	35,9	8,5	7,5	103,8			14,7
	Range	1,2-15	9-17	17-81	3,5-20	4-17	48-1002			2-23

Appendix 4 : Percentage inattentiveness as related with time of day in the incubating red-billed oxpecker observed at 10 different nests in the Satara area in the 1973/74 and 1974/75 breeding seasons.

Time of day	Total minutes inattentive	Percentage inattentive
05h00 - 07h00	5,7	4
07h00 - 09h00	10,3	8
09h00 - 11h00	8,6	6
11h00 - 13h00	9,0	7
13h00 - 15h00	10,3	8
15h00 - 17h00	20,6	16
17h00 - 19h00	23,1	19